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Population ecology of the littoral fringe gastropod Littorina planaxis in Northern California

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POPULATION ECOLOGY OF THE LITTORAL FRINGE GASTROPOD *LITTORINA PLANAXIS* IN NORTHERN CALIFORNIA

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Master of Science

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by

Russell James Schmitt

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POPULATION ECOLOGY OF THE LITTORAL FRINGE GASTROPOD *LITTORINA PLANAXIS* IN NORTHERN CALIFORNIA

ABSTRACT

Life history patterns of individual organisms are the result of natural selection and should be correlated with particular physical and biological characteristics of habitats in which they live. The littoral fringe is known to be the most severe physical habitat in the intertidal zone, and it is expected that organisms in it should have population characteristics associated with selective response to physical adversity rather than biological interaction. Ecological studies of populations of *Littorina planaxis* were made in the Dillon Beach and Bodega Head areas. The study localities differed principally in extent of wave exposure rather than geographical location.

Abundance and population age structure data were obtained for 5 populations of *L. planaxis* over a 12 month period. No seasonal patterns of change were observed. Recruitment was not detected at any site, and analyses of age structure indicated lack of recruitment is not uncommon. A survey of all populations at Dillon Beach in July, 1974, revealed only one with a significant number of young.

Growth data from marked individuals indicate that *L. planaxis* grows slowly (approx. 1mm/yr) and has a long life span (mean age: 11 yrs.). Growth was significantly reduced during the reproductive season. Sexual maturity was attained at a 4.5-5 mm shell length after two to three years of growth.

Breeding season for *L. planaxis* at Bodega Bay lasts from March to early August. A marked semilunar synchrony was observed for copulation and egg release. Laboratory studies indicated snails will spawn during inter-lunar periods after conditioning by immersion. A daily rhythm of oviposition corresponded with each day's higher spring tide. Snails spawned egg capsules with a single ovum. Fecundity was extremely high: a 13 mm snail may spawn 114,000 eggs per season.

All *L. planaxis* populations showed extreme stability in abundance, age structure, growth, and recruitment. The virtual lack of recruitment reflects the physical severity of the environment to the juveniles in terms of access to suitable substrate by settling larvae and subsequent early survival. The data validated Murphy's (1968) predictions based on theoretical considerations that long life, late sexual maturity, and iteroparity are associated with habitats inhospitable to juvenile survival. The inapplicability of r- and K- selection concepts to the populations studied are discussed.

Available data on the reproductive characteristics of the genus Littorina were obtained from published literature and analysed to discover correlations among life history parameters. It was found that littorinids have 4 major reproductive strategies associated with position in the intertidal zone. Major differences between high and low intertidal species were in 1) mode of development, 2) size of the ovum, 3) fecundity, and 4) type of pelagic capsule. High intertidal species tended to have planktotrophic or ovoviviparous development, egg capsules containing a single small ovum, and high fecundity. Initial hypotheses about the adaptive significance of these correlations are:

1) High intertidal species must produce planktotrophic larvae, otherwise the energetic cost of benthic egg production is too high because of the severe environment and the necessity to protect the ova. Ovoviviparity achieves the same end by protecting the developing juvenile within the adult body.

2) High fecundities are imperative in situations where juvenile survival is low if adult population stability is to be maintained.

3) The significance of differences in number of eggs per pelagic capsule is not known, but it is suspected that it is related to conditions in the environment of the larvae and the adult.

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INTRODUCTION

Each different habitat consists of a particular combination of biological and physical conditions which induce specific physiological stresses on organisms (Sanders 1968). The result of natural selection is the evolution of species varying in adaptive responses depending upon the set of environmental stresses affecting the species and its genetic composition (Slobodkin and Sanders 1969). The theoretical and experimental investigation for correlations between specific patterns of stress and life history phenomena provides the foundation for current interest in predicting evolutionary "solutions" or so-called adaptive strategies of organisms. Tinkle (1969) stressed the need for studying life histories and adaptive strategies within a fundamental evolutionary context. Thus, it must be recognized that life history patterns result from the operation of natural selection on individuals in populations, and that data on life history phenomena must be obtained within the context of evolutionary theory.

There are several complimentary approaches to the study of life history phenomena. All center around the hypothesis that organisms possess a finite quantity of time and energy which is optimally partitioned by natural selection among growth, maintenance, and reproduction (Gadgil and Bossert 1970). Moreover, recurrent combinations of physical and biotic variables that induce high mortalities in a species represent strong selection pressure for the evolution of compensatory life history adaptations optimizing survival. Habitats characterized by such combinations should

have suites of species exhibiting similar life histories (Sanders 1968, 1969; Slobodkin and Sanders 1969).

Slobodkin and Sanders (Ibid.) hypothesized that environmental unpredictability was a major factor influencing biological adaptations and species diversity patterns of communities. Habitats subject to both severe and fluctuating conditions have been recognized as having low species diversity since few species can tolerate extreme physical rigors. From a knowledge of environmental characteristics, it should be possible to predict major life history features of the associated biota. Thus, Sutherland (1970) found that non-overlapping populations of the limpet Acmaea scabra in the same locality differed in survival, growth, and recruitment depending upon the position of the population in the intertidal zone. Upper intertidal populations were more stable in abundance, grew faster, and lived longer than lower populations. The differences were attributed to variations in physical and biological conditions in the intertidal zone.

This study is concerned with the population ecology of a high intertidal gastropod, the periwinkle Littorina planaxis Philippi (Gastropoda: Prosobranchia). The purpose of this study was to test some theoretical predictions about the ecology of species living in physically stressful environments. In addition, available data on aspects of the reproductive biology of littorinids were studied in order to discover correlations among life history characteristics of species living at different tidal levels and

to develop hypotheses about reproductive strategies in this family of snails.

With the foregoing theoretical considerations in mind, adaptation of Littorina planaxis to life high in the intertidal zone was studied to determine:

1) the importance of environmental stress in determining life history parameters.
2) the relative importance of physical impact and biological interactions in determining life history patterns.
3) if community parameters such as stability are describable on the basis of life history patterns of individual organisms.

In this study growth rates, seasonal population trends, and reproductive ecology were measured for five populations over a period of twelve months. Results indicate that individual snails grow very slowly and may live for many years. Populations were extremely stable in seasonal abundance and age structure. Mature snails spawned thousands of egg capsules, but recruitment failed at all sites. These results and some initial hypotheses about reproductive life history patterns of this group are presented.

CHARACTERISTICS OF THE LITTORAL FRINGE

As noted by many authors, most organisms are not uniformly distributed over the vertical extent of the rocky intertidal region (see reviews: Lewis 1964; Newell 1970; Connell 1972). Many species occur in one of many horizontal bands found universally along the open coast rocky intertidal zones. One of the major concerns of intertidal ecologists has been to determine the causes of zonation (Stephenson 1942). A leading theory on the maintenance of this zonation is that physical conditions set a species' upper limit while biological interactions determine the lower (Connell 1972).

In rocky intertidal habitats, species diversity decreases in the upshore direction due to increasing physical rigor (Newell op. cit.). The littoral fringe is known to be subject to severe and fluctuating conditions (Newell op. cit.; Lewis op. cit.), and consequently few species are found there (Colman 1933). Catastrophic mortalities of high intertidal limpets have been documented by Sutherland (1970), Frank (1965), and Lewis (1954) due to high temperatures. Frank (op. cit.) reported mortality from winter freezes when large sections of rock bearing limpets were sloughed off by frost heave.

The diversity of intertidal organisms along the coast of northern California is unusually high for this latitude (38°15'N), and is caused by nearshore upwelling (Ricketts, Calvin, and Hedgpeth 1969). Compared with the rich and productive biota found in other

regions of the intertidal zone, the littoral fringe supports relatively few species. The common grey periwinkle, Littorina planaxis, is the dominant faunal representative. The ranges of three other gastropod species extend marginally into this region: Littorina scutulata, Acmaea digitalis, and A. scabra. The isopod, Ligia occidentalis, was commonly found occupying fissures with L. planaxis. The barnacle zone, including the species Cthamalus dalli, Balanus glandula, and B. cariosus, marked the lower extreme of the littoral fringe. Microscopic algae identified by Foster (1964) for the littoral fringe near Pacific Grove, California, include the following species: Green algae: Spongomorpha coalita, Endocladia testarum; Blue-green: Plectonema terebrans, Calothrix pilosa, C. crustacea, Dermocarpa sp., Spirulina sp.; and Red algae: Rhodochorton rothii. The filamentous algae, Enteromorpha sp., was found in littoral fringe areas associated with freshwater rivulets.

Species inhabiting the upper reaches of the intertidal zone are subject to prolonged exposure to climatological conditions. During the past five years, mean monthly air temperatures at Dillon Beach, Marin Co., California ranged from a high of 65°F (18.5°C) in October to a low of 40°F (4°C) in December (Figure 1). Two seasons can be recognized by amount of rainfall. The wet season (Oct.-Apr.) has on the average 33.7 inches of precipitation while the dry season (May-Sept.) received 2.2 inches (Figure 2). Mean monthly surf temperatures varied from 10.6°C in December to 15.2°C in September (Figure 3).

During the 12 months of this study, weather conditions varied

slightly from the previous five year mean. Air temperatures were at least three degrees warmer than average during June, July, October, and November 1973. Rainfall deviated significantly from the grand mean. The wet season received more rainfall (53.7") and the dry season less (1.7"). There was no appreciable difference between 1973-74 monthly mean surf temperatures and the five year mean. The maximum daily air temperature was 90 F (32.5°C) on September 27, 1973, and the minimum air temperature was 32°F (0°C) on January 2, 1974.

The tides along this coast are of the mixed semi-diurnal type with a 25-hour time lag between corresponding phases (Daetwyler 1966). The maximum tidal amplitude is 8.7 feet and the mean range is 5.75 feet.

Figure 1. Mean monthly maximum and minimum air temperatures at the Pacific Marine Station, Dillon Beach, California. Solid line represents 1973-74 temperatures and dashed line is the previous five year grand mean (1967-1972).

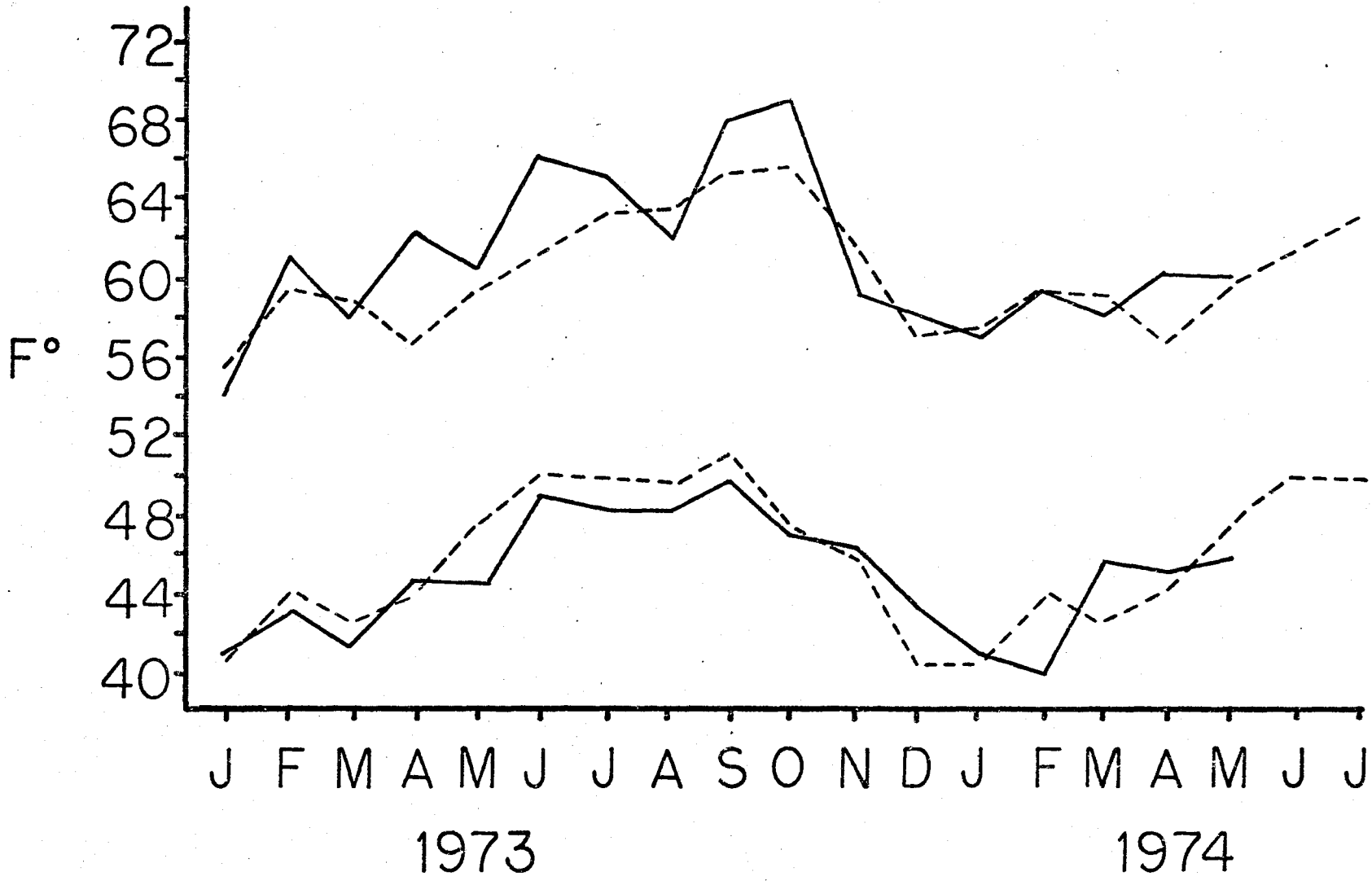

72
68
64
60
F°
56
52
48
44
40
J F M A M J J A S O N D J F M A M J J
1973
1974

Figure 2. Mean monthly inches of precipitation at the Pacific Marine Station, Dillon Beach, California. Solid line represents the 1973-74 rainfall and the dashed line is the previous five year grand mean (1967-1972).

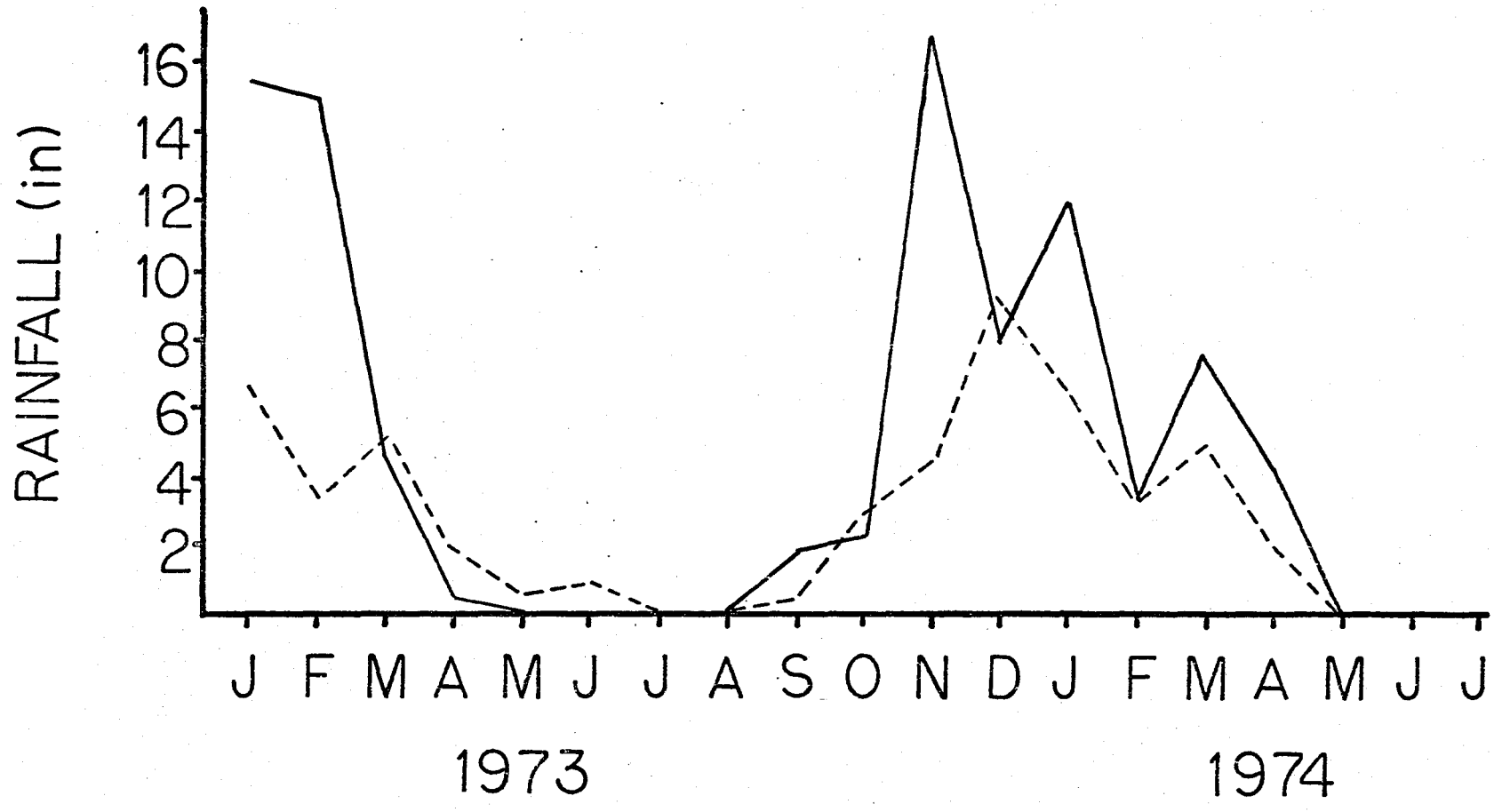
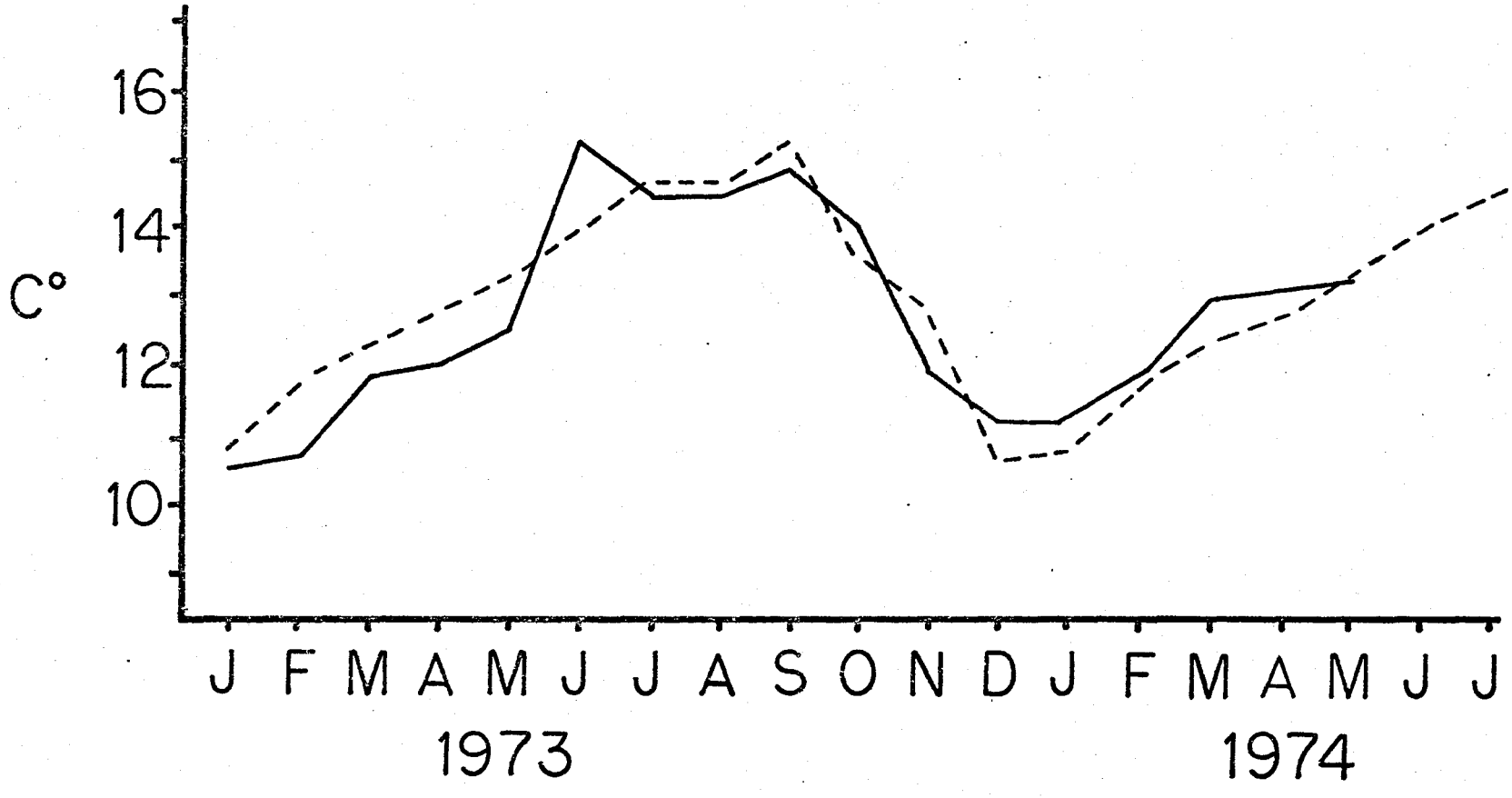

RAINFALL (in)
16
14
12
10
8
6
4
2
J F M A M J J A S O N D J F M A M J J
1973
1974

Figure 3. Mean monthly surf temperature at the Pacific Marine Station, Dillon Beach, California. Solid line represents 1973-74 temperatures and the dashed line is the previous five year grand mean (1967-1972).


C°
16
14
12
10
J F M A M J J A S O N D J F M A M J J
1973
1974

POPULATION DYNAMICS

Study Sites

Seasonal estimates of snail abundance and population age structure were made over a 12 month period at five study sites. Two areas were located on Bodega Head 1.5 miles south of the Bodega Marine Laboratory of the University of California. The three Dillon Beach localities were approximately one-half mile north of the Pacific Marine Station of the University of the Pacific (Figures 4 & 5). The areas were chosen to represent the local variation in "typical" Littorina planaxis habitats, differing principally in extent of wave exposure rather than geographical location. The major features of each area are as follows:

Dillon Beach Site 1: All Dillon Beach sites are described as protected outer coast (Ricketts, Calvin, and Hedgpeth 1969). This area was a vertical south-facing wall 8 meters long by 6 meters high. A large fissure bisected the rock: many L. planaxis aggregated there. Several large Pachygrapsus crassipes crabs also inhabited the crevice. Tidal height of the lowest quadrat containing L. planaxis was +5 feet. Based on observation at high tide, this site was ranked third in amount of wave splash received. Barnacles and limpets were abundant on the lower third of the rock.

Dillon Beach Site 2: Located on a west-facing vertical wall of a large boulder, this site received the most wave splash of any area. This boulder was estimated to be 6 meters high with a diameter of 5 meters. Snails were found as high as +14 feet. Barnacles were scarce,

but limpets were large and abundant.

Dillon Beach Site 3: This site was a south-facing wall on the same boulder as Dillon Beach Site 2. Ranked fourth in amount of splash received, the upper-most snails were found at +10 feet. This site and DB Site 2 represented the same population in two subhabitats. Limpets were abundant, but more barnacles were found here than DB Site 2.

Bodega Head Site 1: Both Bodega Head sites were located on the open coast, although this area was the most protected from wave splash. The area was a long gently sloping south-facing bench. Snails were found in a narrow band approximately +5 to +7 feet. Freshwater ran through the center of this site from February to April 1974, causing a thick growth of Enteromorpha sp. Littorina scutulata associated with L. planaxis at this site were the largest observed, some reaching 18 mm in shell length. Many L. scutulata, barnacles, and limpets occupied positions in lower half of bench.

Bodega Head Site 2: A vertical south-west facing wall, this area received the second greatest amount of wave splash. Located on the open coast, the area was protected to some degree by a large offshore boulder. The upper limit of L. planaxis was approximately +17 feet. Many narrow fissures transected the rock face. The fissures were occupied by small L. planaxis.

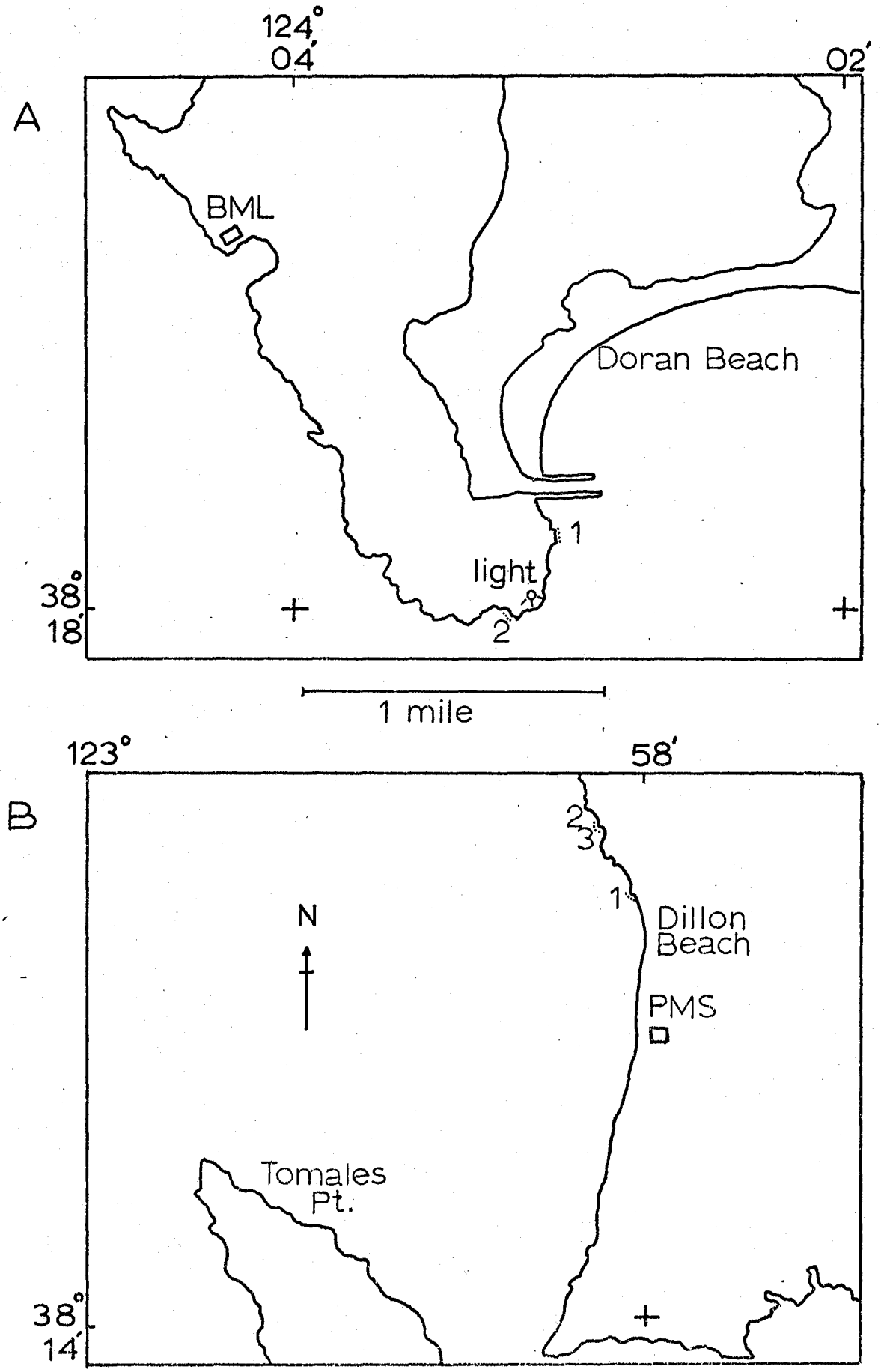
Figure 4. General view of Littornia planaxis sampling areas showing relative positions of Bodega Head and Dillon Beach.

	0	1	2	3	4	5	6	7	8	9
0			27		3 meas.	0				
1				16 meas.		4	1			
2		27 meas.	31					0		
3			27 meas.			7		3		
4			24		21		18 meas.			
5	4 meas.	0			8					

A. *Littorina planaxis* sampling areas on Bodega Head.

Figure 5.

B. *Littorina planaxis* sampling areas at Dillon Beach.


A
124°
04′
02′
BML
Doran Beach
1
light
2
38°
18′
1 mile
B
123°
58′
2
3
1
N
Dillon
Beach
PMS
Tomales
Pt.
38°
14′

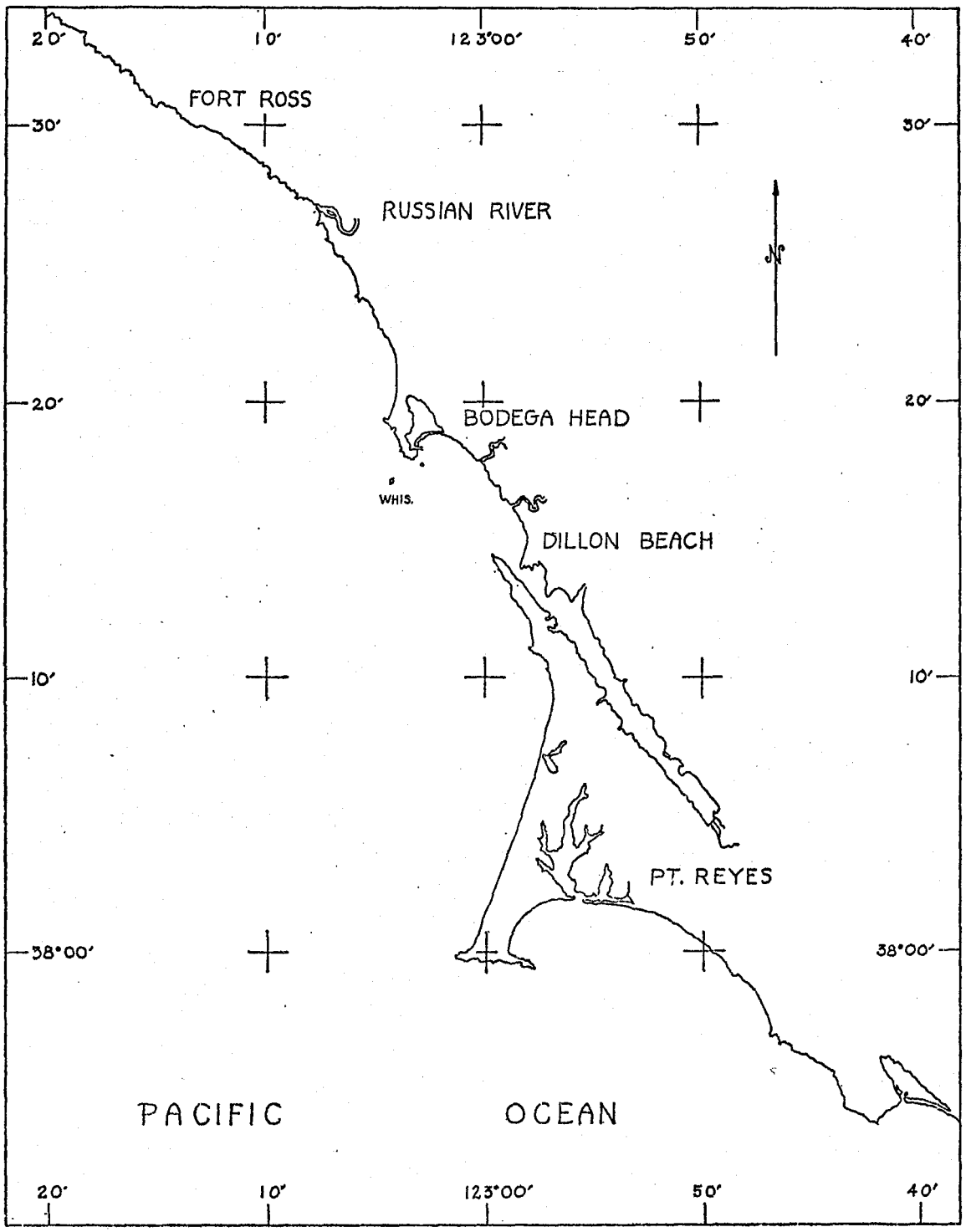
Methods

Ecological data on Littorina planaxis were obtained from the study areas by sampling once each month. Sixty permanent quadrats (.66m X .66m) were established at each site. A vertical transect through the range of L. planaxis was split into six .66 meter tidal intervals (approximately 2 foot heights). Each height was partitioned into ten .66 meter quadrats. If a quadrat was to be sampled, a $\frac{1}{4}^2$ meter grid was placed randomly within it (Figure 6).

Stratified random sampling was used. Snails from three $\frac{1}{4}^2$ meter grids were counted in each tidal level, making a total of 18 abundance counts per area each month. Coordinates of the quadrats to be sampled were picked from a random number table. Snails from one $\frac{1}{4}^2$ meter grid at each tidal height were measured (maximum shell length). The six grids chosen for size data corresponded to the first set of coordinates picked from the random number table for each level. Shell length was measured to the nearest .5mm with vernier calipers.

Statistical techniques used in this study are from Sokal and Rohlf (1969) unless otherwise stated. Calculations were made on a Wang 500 computer.

Figure 6. Graphic illustration of monthly sampling procedure. The numbers along the top and side represent coordinates of the quadrats. Snails from three quadrats in each tidal level were counted (numbers in squares). Snails found in the first quadrat coordinates of each tidal level were measured (indicated on graph). This table represents the Bodega Head Site 2 sample from July 7, 1974.


20'
10'
123°00'
50'
40'
FORT ROSS
30'
RUSSIAN RIVER
N
20'
BODEGA HEAD
WHIS.
DILLON BEACH
10'
PT. REYES
38°00'
PACIFIC
OCEAN

Abundance

Monthly estimates of abundance were made by averaging the number of snails found in the eighteen quadrats for each area. The population abundances were remarkably stable during the twelve months of the study (Figures 7-11). The striking numerical stability is evidenced by the consistent enclosure of the overall yearly average in the 50% confidence limits for monthly means.[1] Only 14 (23%) of the 61 total observations had 50% confidence intervals that did not include the overall mean.

Large fluctuations in density did not occur within populations on a seasonal basis. Abundance did vary significantly from area to area (ANOVA: F_s=48.15; df. 4,∞; $p<.001$). Yearly estimates of Littornia planaxis abundances ranged from a high of 55.9/m^2 at Bodega Head Site 2 to the 11.1/m^2 low at Bodega Head Site 1. Dillon Beach areas had densities of 31.6/m^2 (DB1), 44.4/m^2 (DB2), and 14.0/m^2 (DB3). The two areas receiving the least amount of wave splash at high tide had the lowest densities (Bodega Head Site 1 and Dillon Beach Site 3).

The variation in abundance between Dillon Beach areas 2 and 3 are probably due to differences in the physical environment

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1 50% confidence intervals reduce the region of acceptance for the null hypothesis (abundance does not vary seasonally). The enclosure of the true mean by the 50% intervals is expected 50 times out of 100. In this case, only 23 of the 100 fall in the rejection region, indicating highly stable seasonal abundance.

as these sites represent the same population in two sub-habitats. The south-facing side (DB3) had much different splash characteristics, and very little moisture was received at high tide. The west surface (DB2) received the brunt of a wave's impact. Sutherland (1970) reported that the reduced densities of high intertidal populations of Acmaea scabra were the result of a more severe physical environment.

Data for each tidal level was averaged to give abundance estimates for tidal position. Table 1 clearly shows that Littorina planaxis is not uniformly distributed throughout its vertical range. With the exception of Bodega Head Site 2, maximum snail abundance occurred near the center of the distribution, trailing off toward both extremes. The Bodega Head population was more evenly distributed.

Figure 7. Estimates of population abundance for Dillon Beach Site 1. Circle represents monthly mean, box the 50% confidence interval, the solid vertical line the 95% confidence interval, and the dashed line the yearly mean.

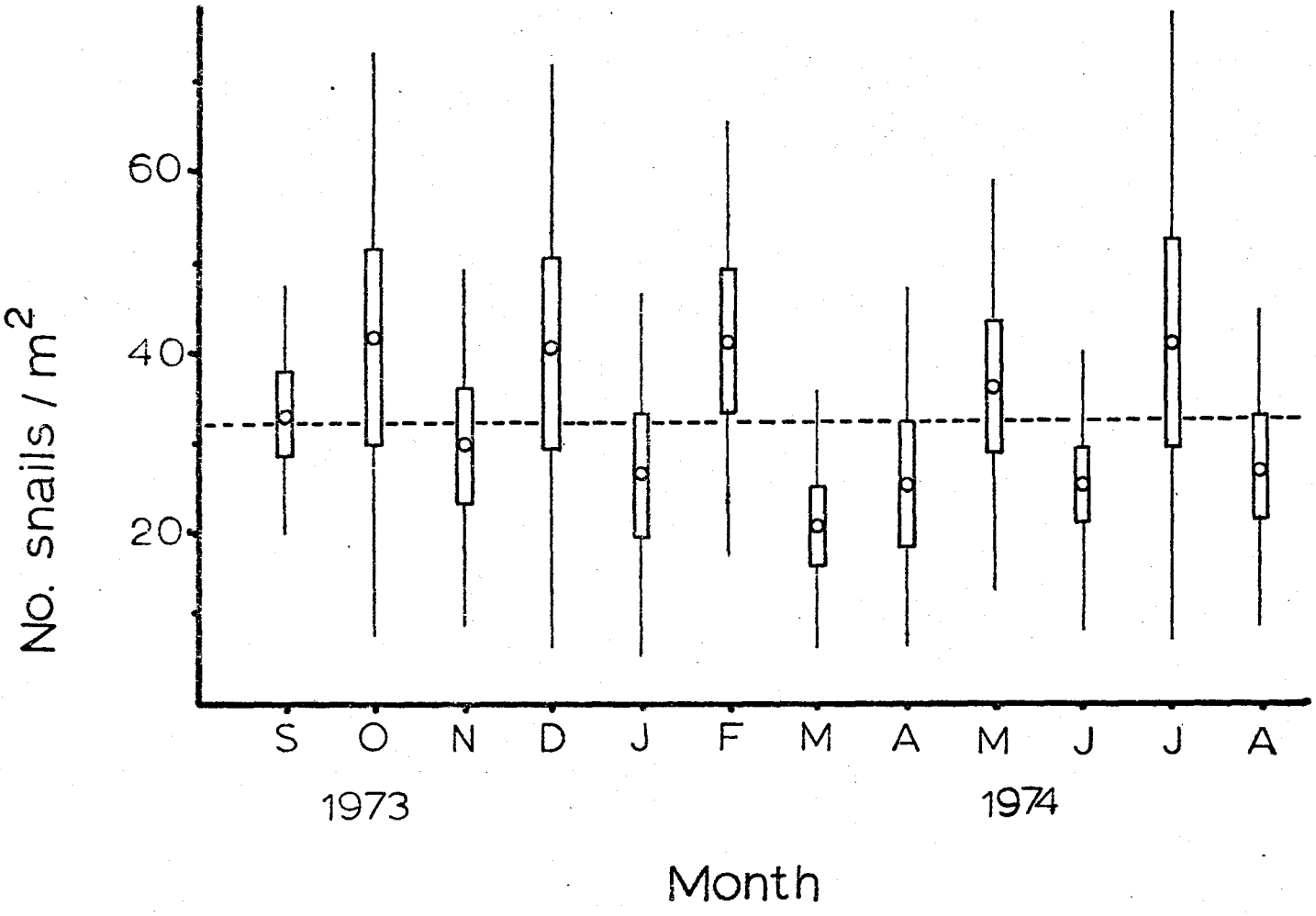

No. snails / m²
60
40
20
S
O
N
D
J
F
M
A
M
J
J
A
1973
1974
Month

Figure 8. Estimates of population abundance for Dillon Beach Site 2. Symbols as in Figure 7.

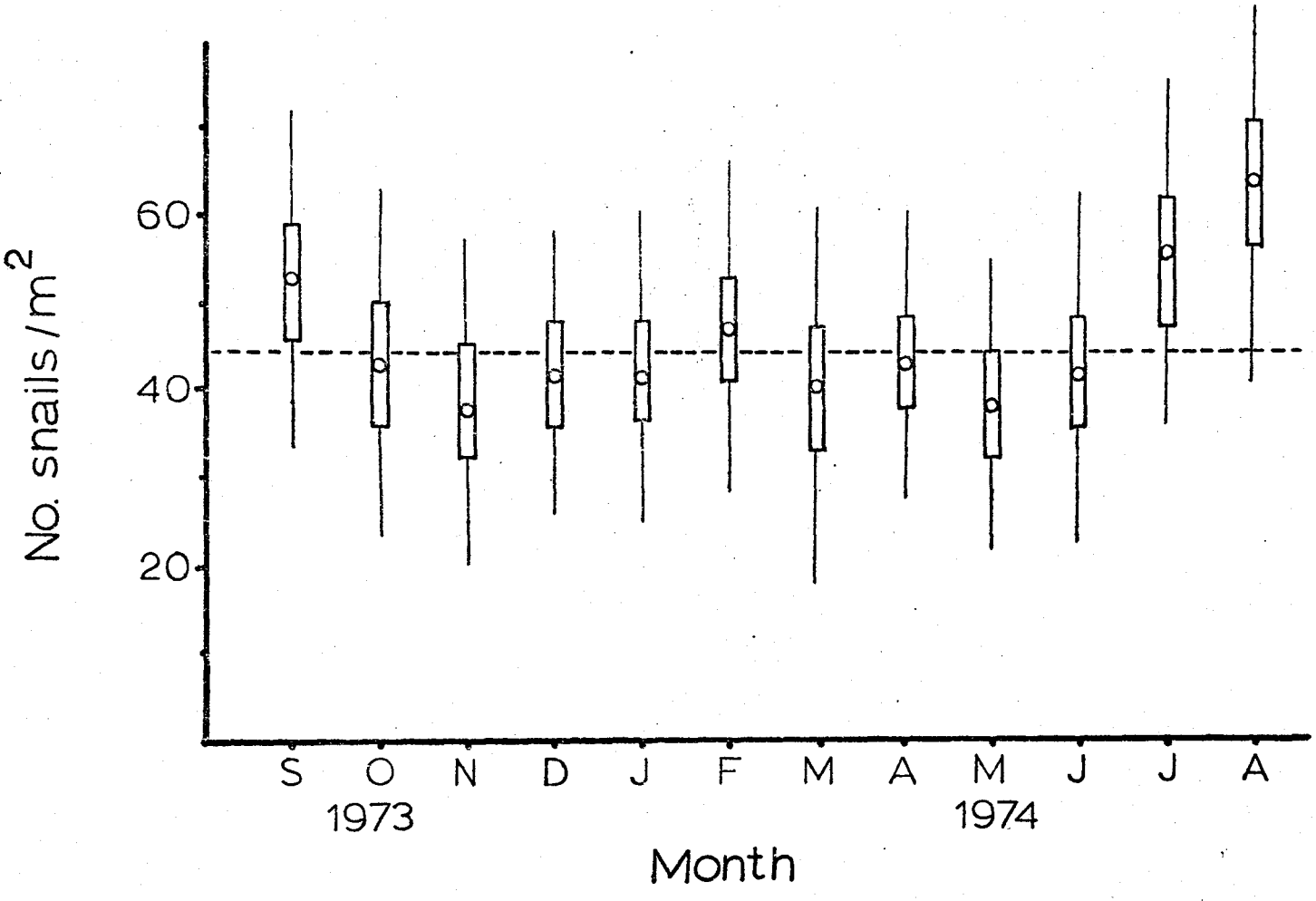

No. snails / m²
60
40
20
S
O
N
D
J
F
M
A
M
J
J
A
1973
1974
Month

Figure 9. Estimates of population abundance for Dillon Beach Site 3. Symbols as in Figure 7.

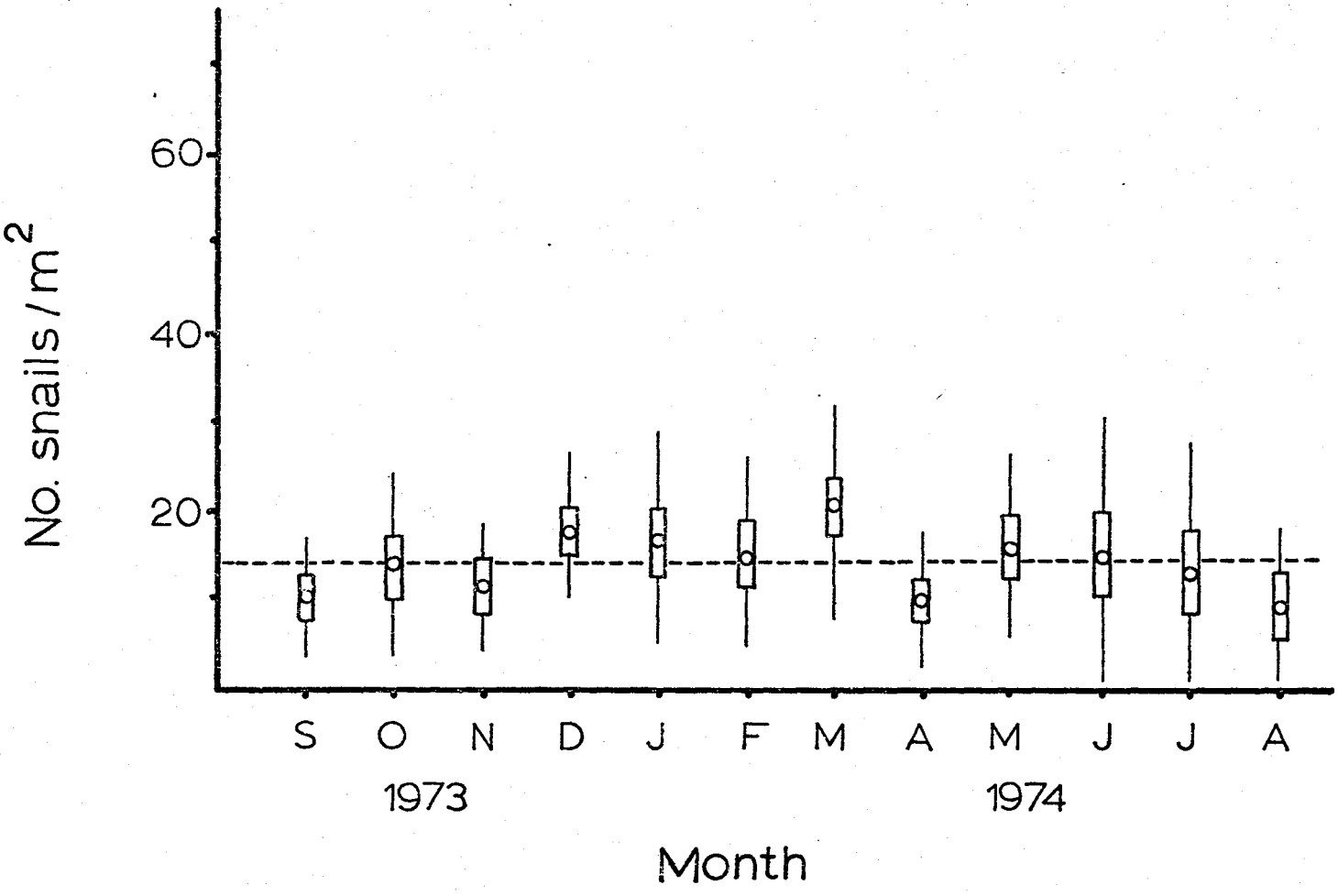

No. snails / m2
60
40
20
S
O
N
D
J
F
M
A
M
J
J
A
1973
1974
Month

Figure 10. Estimates of population abundance for Bodega Head Site 1. Symbols as in Figure 7.

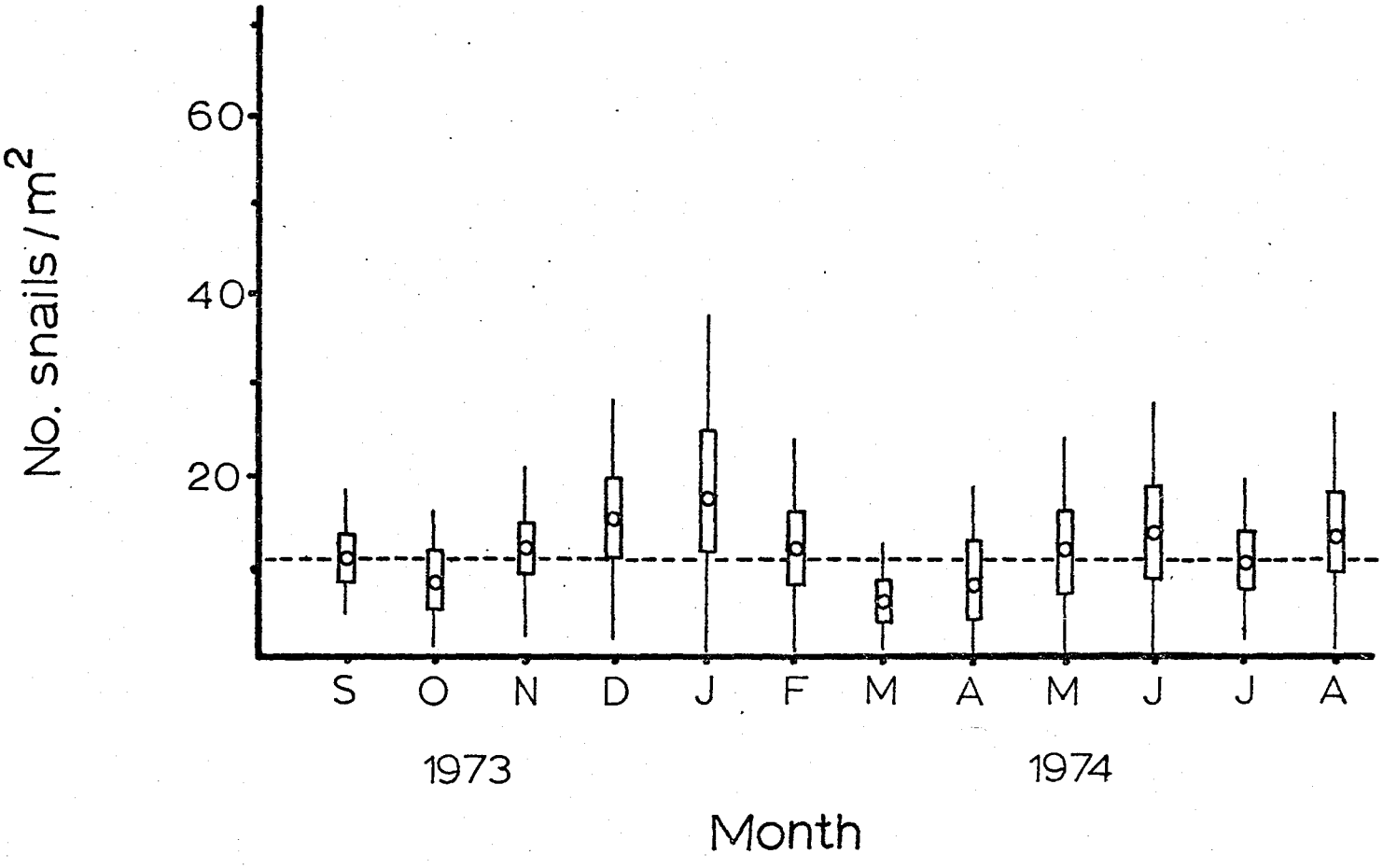

No. snails / m2
60
40
20
S
O
N
D
J
F
M
A
M
J
J
A
1973
1974
Month

Figure 11. Estimates of population abundance for Bodega Head Site 2. Symbols as in Figure 7.

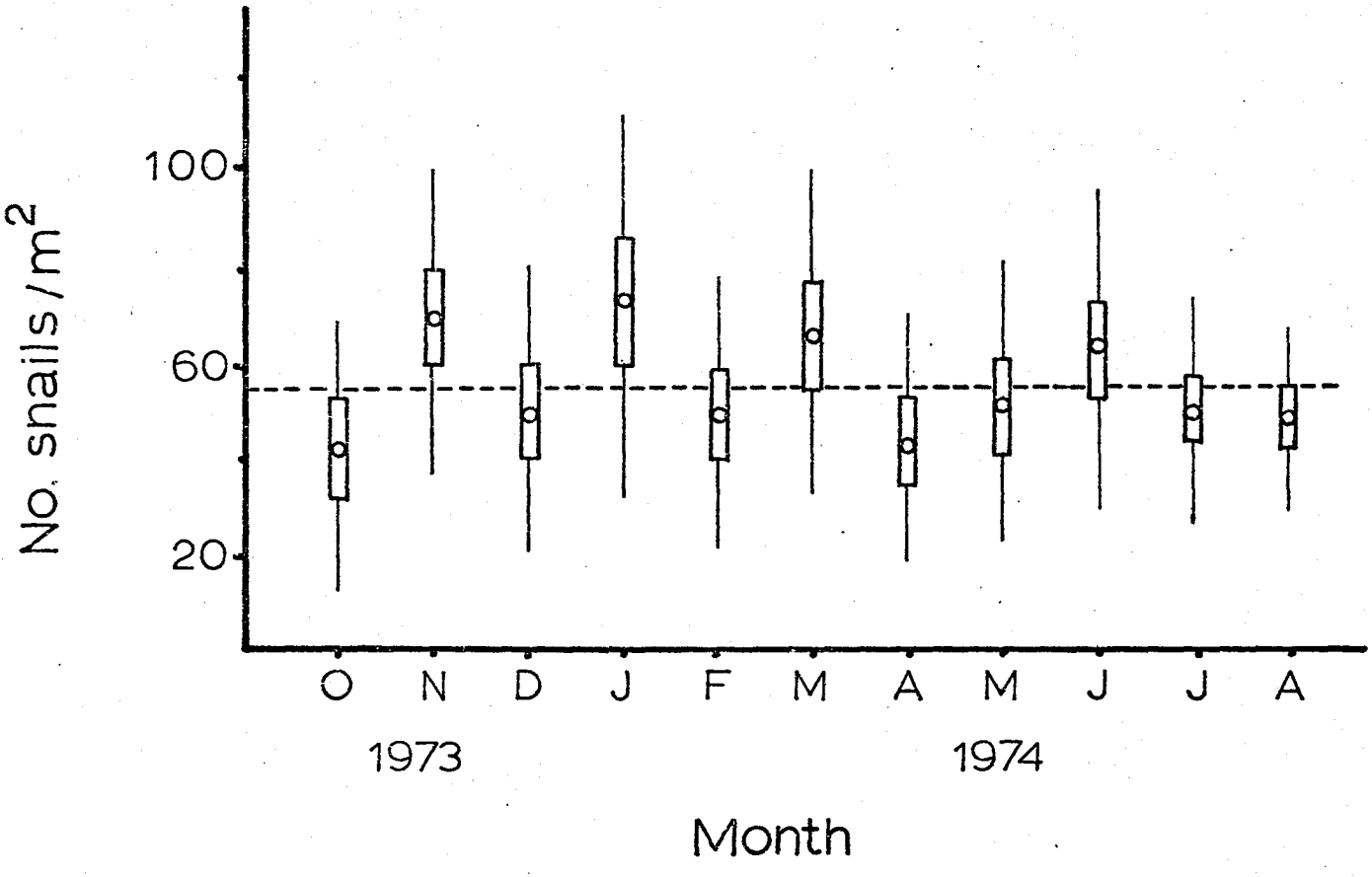

No. snails / m2
100
60
20
O
N
D
J
F
M
A
M
J
J
A
1973
1974
Month

Table 1

VERTICAL DISTRIBUTION

Locality Tidal level	Abundance/m^2	Relative Frequency	N
Dillon Beach Site 1			1187
0 (highest)	.11	.001	1
1	23.00	.17	207
2	64.20	.49	578
3	40.33	.31	363
4	4.10	.03	37
5 (lowest)	.11	.001	1
Dillon Beach Site 2			2080
0	30.17	.13	264
1	59.54	.25	521
2	82.51	.35	722
3	53.94	.23	472
4	10.63	.05	93
5	.91	.001	8
Dillon Beach Site 3			527
0	.80	.01	7
1	7.31	.12	64
2	26.63	.44	233
3	16.00	.27	140
4	9.26	.15	81
5	.23	.001	2
Bodega Head Site 1			510
0	6.40	.11	56
1	6.17	.11	54
2	15.77	.27	138
3	21.94	.38	192
4	7.31	.13	64
5	.69	.01	6
Bodega Head Site 2			2525
0	53.33	.16	400
1	53.47	.16	401
2	61.87	.18	464
3	63.07	.19	473
4	77.20	.23	579
5	27.73	.08	208

Mean Size of Snail

Unlike the extremely stable abundance pattern, monthly mean size of snail did vary (Figures 12-16). Paired comparison of consecutive sampling periods were analyzed for differences with Student's t-Test. Results, presented in Table 2, indicate no single seasonal pattern of change for the five populations. A total of 20 (33%) of the 61 estimates differed. However, only 10 (16.7%) of the monthly means did not include the overall yearly mean in their 95% confidence intervals. This low number of significant differences is not much larger than expected based on the number of snails measured at each area per month (range: 30-222) and the number of tests performed. The remaining variance could be accounted for by a non-random size distribution.

Mean size of snail varied considerably between populations. Snails at Dillon Beach averaged 10.9mm (DB1), 12.4mm (DB2), and 12.8mm (DB3) in shell length. The two Bodega Head populations were 14.9mm (BH1) and 11.2mm (BH2) in length. A Student-Newman-Keuls test indicated that all yearly means differed ($p<.05$).

To investigate the relative contribution of small size classes to the overall mean, monthly averages were recalculated ignoring snails in 2 to 6.9mm size range. The original mean was tested against this recalculated mean with Student's t-Test. Significant differences are tabulated in Table 3. The results show that small

sizes have only a minor influence on mean size, a finding consistent with the predominance of older snails in most populations (see Size-frequency section). In the two areas with appreciable numbers of young snails (Dillon Beach Site 1 and Bodega Head Site 2) significant changes in size were detected.

Figure 12. Monthly mean shell length for snails at Dillon Beach Site 1. Circles represent monthly means, vertical lines the 95% confidence intervals, and the dashed line the overall yearly mean.

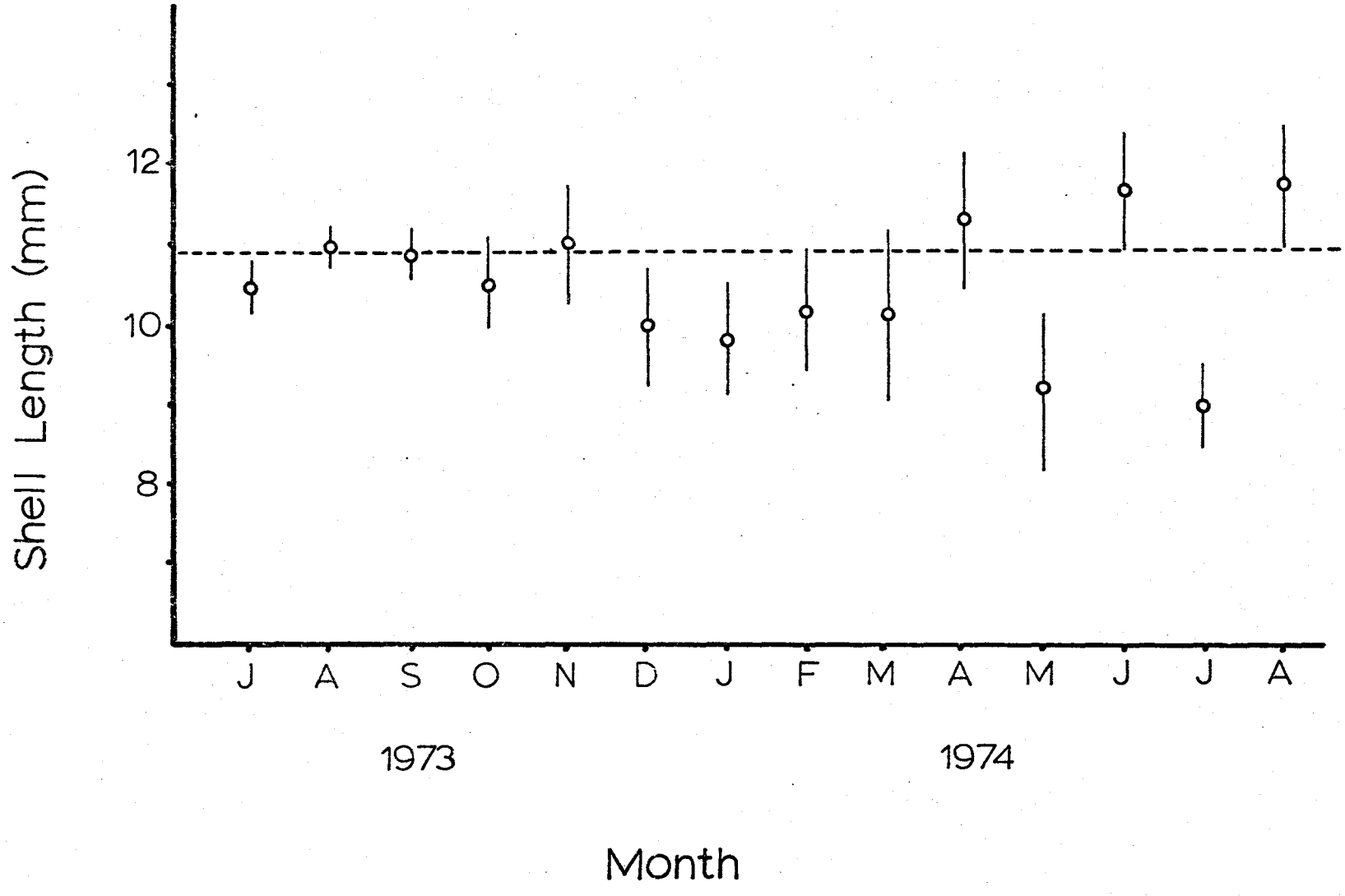

Shell Length (mm)
12
10
8
J
A
S
O
N
D
J
F
M
A
M
J
J
A
1973
1974
Month

Figure 13. Monthly mean shell length for snails at Dillon Beach Site 2. Symbols as in Figure 12.

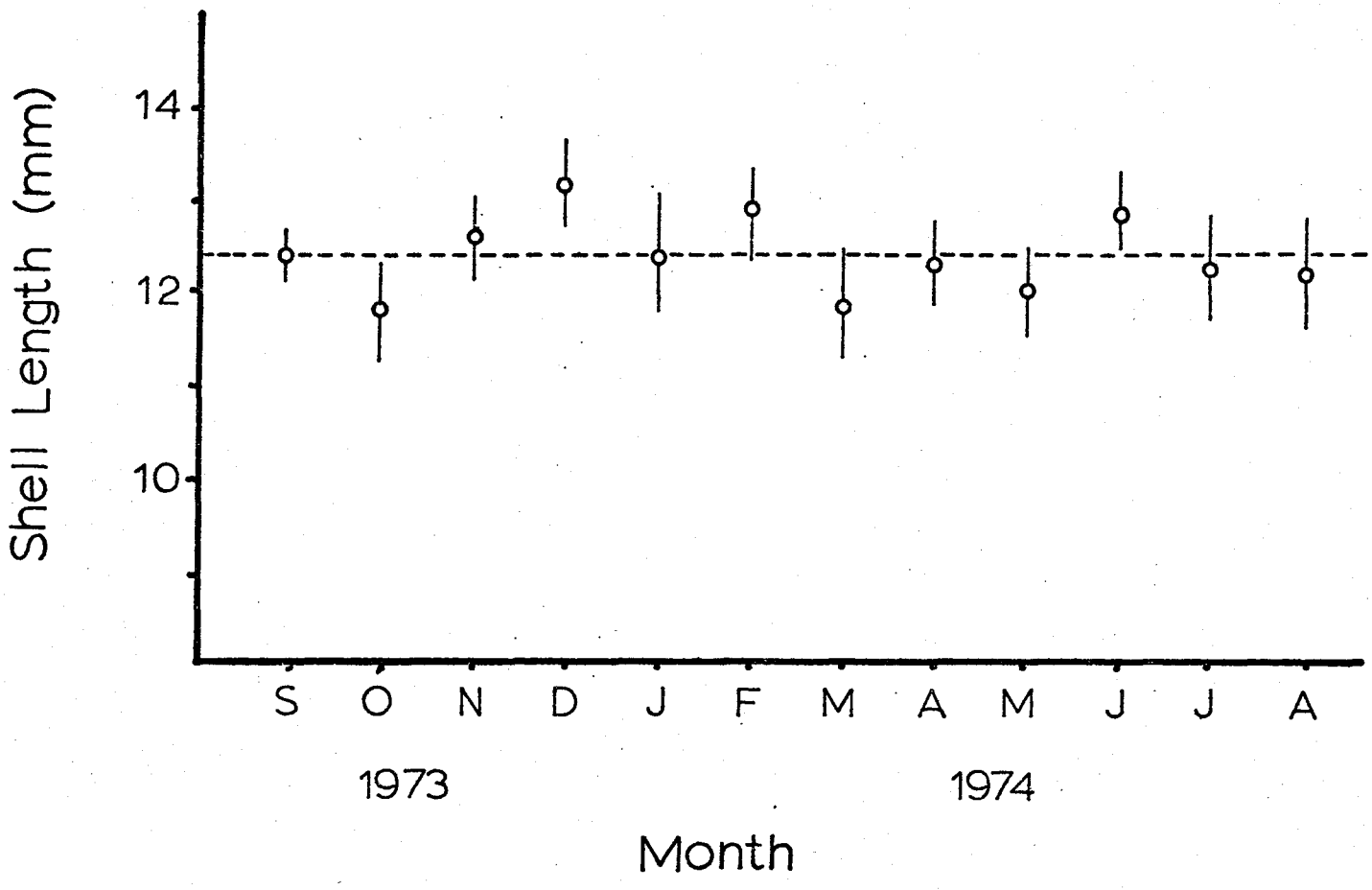

Shell Length (mm)
14
12
10
S
O
N
D
J
F
M
A
M
J
J
A
1973
1974
Month

Figure 14. Monthly mean shell length for snails at Dillon Beach Site 3. Symbols as in Figure 12.

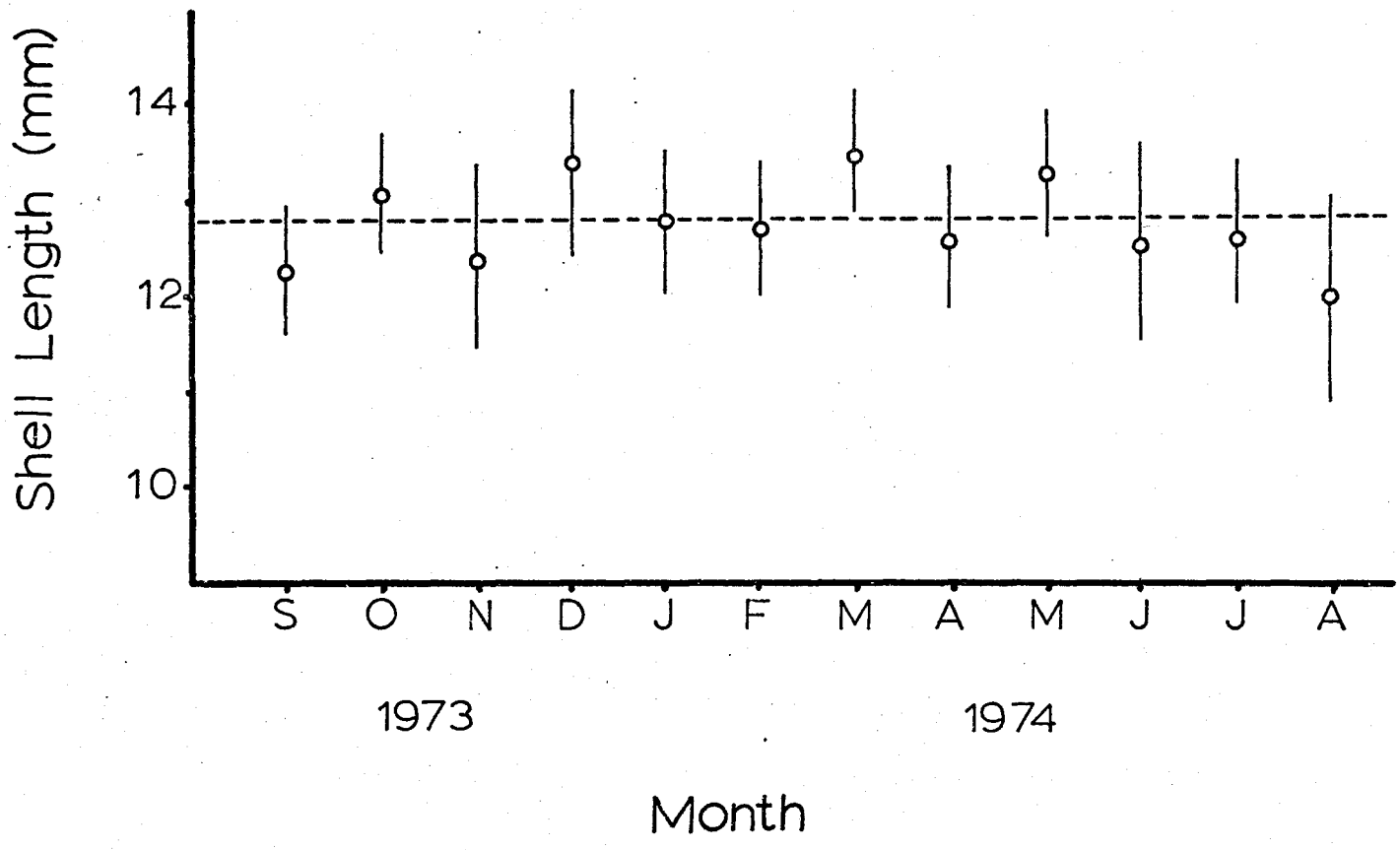

Shell Length (mm)
14
12
10
S
O
N
D
J
F
M
A
M
J
J
A
1973
1974
Month

Figure 15. Monthly mean shell length for snails at Bodega Head Site 1. Symbols as in Figure 12.

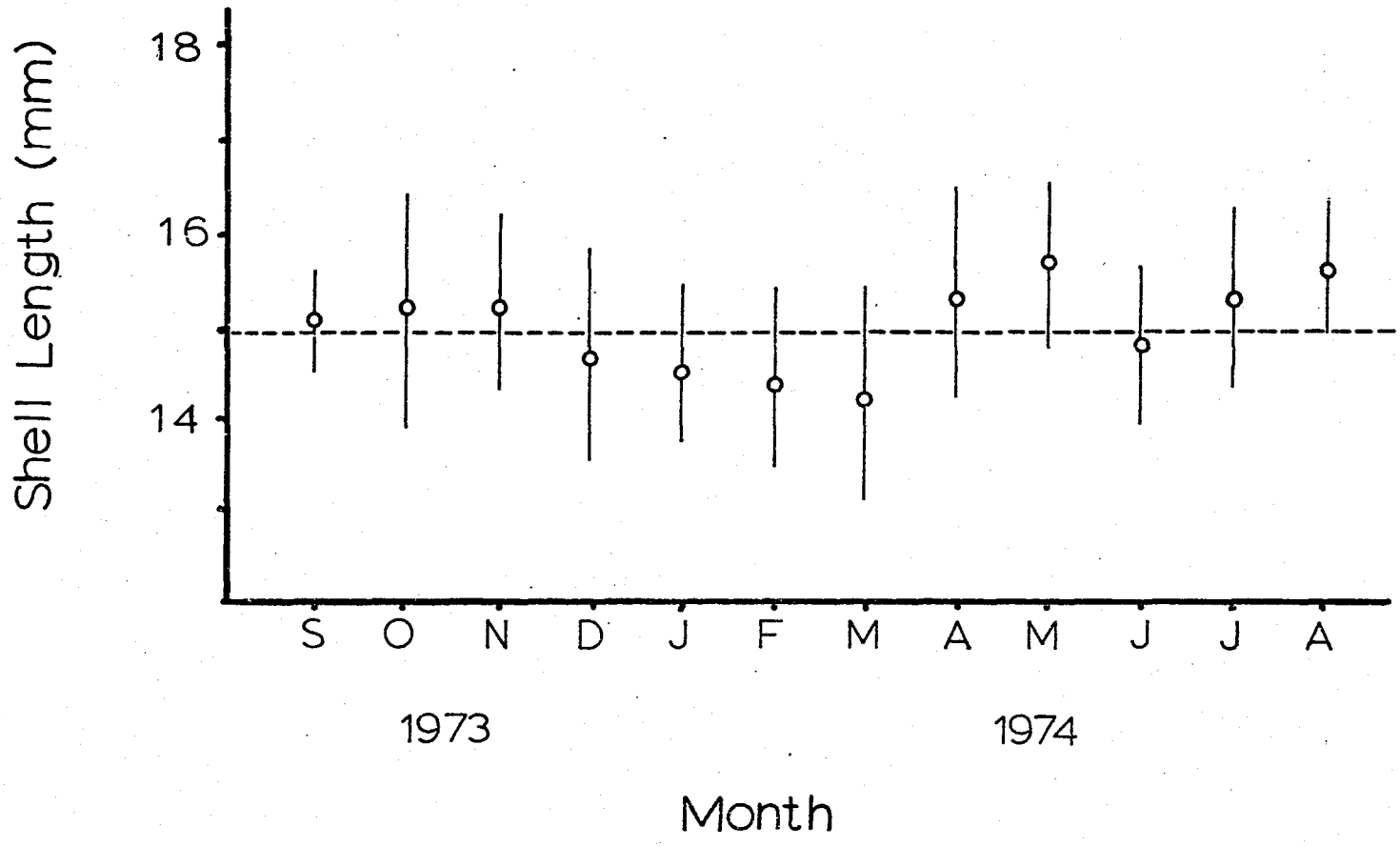

Shell Length (mm)
18
16
14
S
O
N
D
J
F
M
A
M
J
J
A
1973
1974
Month

Figure 16. Monthly mean shell length for snails at Bodega Head Site 2. Symbols as in Figure 12.

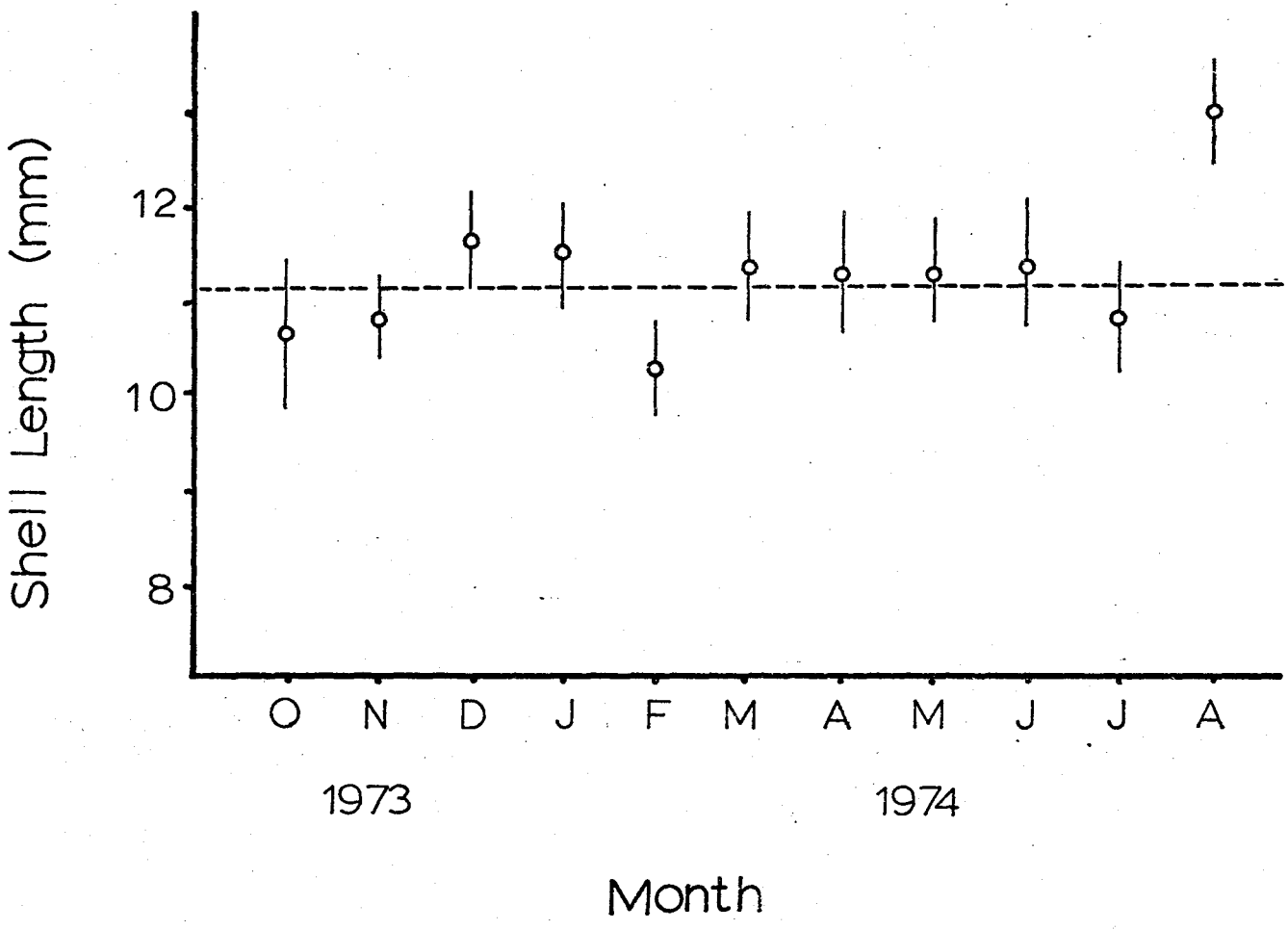

Shell Length (mm)
12
10
8
O
N
D
J
F
M
A
M
J
J
A
1973
1974
Month

Table 2: Analysis of mean size snail for consecutive sampling periods. This is a one tailed Student's t-Test. Only significant differences are indicated.

Location	Sampling period	Level of significance	Direction of change
Dillon Beach Site 1			
	July - August 1973	$p<.001$	August larger
	Sept. - October	$p<.05$	October smaller
	Nov. - December	$p<.025$	December smaller
	March - April 1974	$p<.05$	April larger
	April - May	$p<.001$	May smaller
	May - June	$p<.001$	June larger
	June - July	$p<.001$	July larger
Dillon Beach Site 2			
	Sept. - October	$p<.01$	October smaller
	Oct. - November	$p<.025$	November larger
	Nov. - December	$p<.025$	December larger
	Dec. - January	$p<.025$	January smaller
	Feb. - March	$p<.01$	March smaller
	May - June	$p<.025$	June smaller
Dillon Beach Site 3			
	Feb. - March	$p<.05$	March larger
	March - April	$p<.05$	April smaller
Bodega Head Site 2			
	Nov. - December	$p<.01$	December larger
	Jan. - February	$p<.01$	February smaller
	Feb. - March	$p<.01$	March larger

Table 3: Comparison of monthly means with and without 2 to 6.9mm size classes. This is a two tailed Student's t-Test. Only significant differences are noted.

Location	Month	True Mean	Test Mean	Level of significance
Dillon Beach Site 1				
	July 1973	10.55mm	10.97mm	$p < .01$
	August	11.06	11.35	$p < .05$
	July 1974	9.00	10.08	$p < .01$
Bodega Head Site 2				
	February 1974	10.30mm	11.38mm	$p < .01$
	May	11.33	12.32	$p < .01$
	June	11.44	12.55	$p < .01$
	July	10.76	11.72	$p < .05$

Size-Frequency Distribution: Recruitment

Figures 17-21 graphically represent the size-frequency distributions of Littornia planaxis at the five study localities. The plots clearly illustrate the paucity of smaller sized snails in most areas throughout the year. All populations were composed of several distinct size components, although two generalized distribution curves can be seen.

Dillon Beach Site 1 and Bodega Head Site 2 populations displayed normal shaped curves with maximum number of snails in middle sizes. The other three populations showed differing degrees of skewness towards larger sizes. The presence of two size distribution curves suggests populations having different dynamics. For example, a stable population might be expected to display the following attributes: 1) stable seasonal abundance, 2) recruitment equal to mortality, and 3) a larger number of individuals in middle size classes. A declining population with low adult mortality may be expected to show: 1) stable seasonal abundance, declining slightly, 2) recruitment rate below mortality rate, and 3) disproportionally more older individuals.

Connell (1972) pointed out that changes in severity of physical conditions will often have a profound effect on a population's age structure. Thus, Sutherland (1970) found high populations of Acmaea scabra to consist primarily of four-year-old snails. Lower populations had a complete complement of smaller size classes. Connell (1961b) described dominant year classes for populations of Balanus balanoides

in physically rigorous areas.

The predominance of large size snails in the present study fits well with Connell's concept of a physically influenced population structure. Furthermore, since the study areas represented a gradient of physical conditions, size-frequency plots of a particular site corresponded to the expected distribution. The populations that received little wave splash (Dillon Beach Site 3 and Bodega Head Site 1) were composed of larger snails. The smallest consistently present size class (observed in half of the twelve monthly samples) was 10mm in shell length. This size corresponds to approximately 8 to 9 years of growth (see Growth section). Four and five millimeter snails were consistently present at the other areas. These sizes are attained after one and a half to two years of growth.

Recruitment of young Littornia planaxis was never observed en masse. One-year-old snails (3.0mm) were found at Dillon Beach Site 1 and Bodega Head Site 2, but were only seen in the fall and spring months at Dillon Beach Site 1. The paucity of juvenile snails coupled with the stable abundance and mean size patterns indicate low recruitment of L. planaxis during this study. It cannot be fully determined if this low magnitude is representative of previous years. However, population age structure suggests that low recruitment, or even complete reproductive failure, may be quite common.

North (1954) monitored one population near La Jolla, California, that averaged 4mm in shell length throughout the 24 month study.

Snails in this size range were very rare at most sites. Three explanations for the lack of these smaller classes are as follows: 1) these sizes did not exist (i.e., recurrent recruitment failure), 2) small snails were missed during monthly sampling, or 3) young occupy different portions of the habitat than old snails.

The sampling methods utilized did not underestimate numbers of smaller snails. First, juvenile snails were found regularly at two study sites. There was no problem noting the smallest snails. Bock and Johnson (1967) described similar size structure for populations of Littorina planaxis at Doran Beach and Bodega Head, California. The results obtained from monthly sampling here were probably due to a general lack of young individuals rather than sampling error.

A comprehensive survey of the rocky intertidal littoral fringe at Dillon Beach during July, 1974, lends credence to the third alternative: habitat partitioning when smaller sizes exist. One population was found to have a significant fraction of snails in 3 to 6mm size classes. Though most members of this population inhabited the area of rock available to them (approx. 12^2 meters), the vast majority of smaller snails were located within a section measuring two square meters. Additionally, the topography of this area differed considerably from the adult sections.

The rock section containing the juveniles was approximately two meters removed from the remaining population, though a few snails were found on a flat bench connecting the two areas. In addition to being slightly upshore, the "nursery" section was well protected from

the full force of wave splash. The area was, however, liberally wetted at high tide. The nursery itself was a slightly sloping extension of the flat bench, well pitted with small holes (3-7mm wide; 5-25mm deep). Snails were found only within these holes. Veligers would presumably settle out in small tide pools left on the bench after high tides.

Snails were measured in three line transects (1 meter by 10cm) placed horizontally through both the nursery and control populations. Results are presented as size-frequency distributions in Figure 22. It is interesting to note that the size-frequency plot for the combined data is one of the few bimodal distributions observed in this study. Mean size of snail was 7.27mm (SD 2.28) in the nursery, and 11.38mm (SD 2.92) for the control population.

Figure 17. Size-frequency distributions of *Littorina planaxis* at Dillon Beach Site 1.

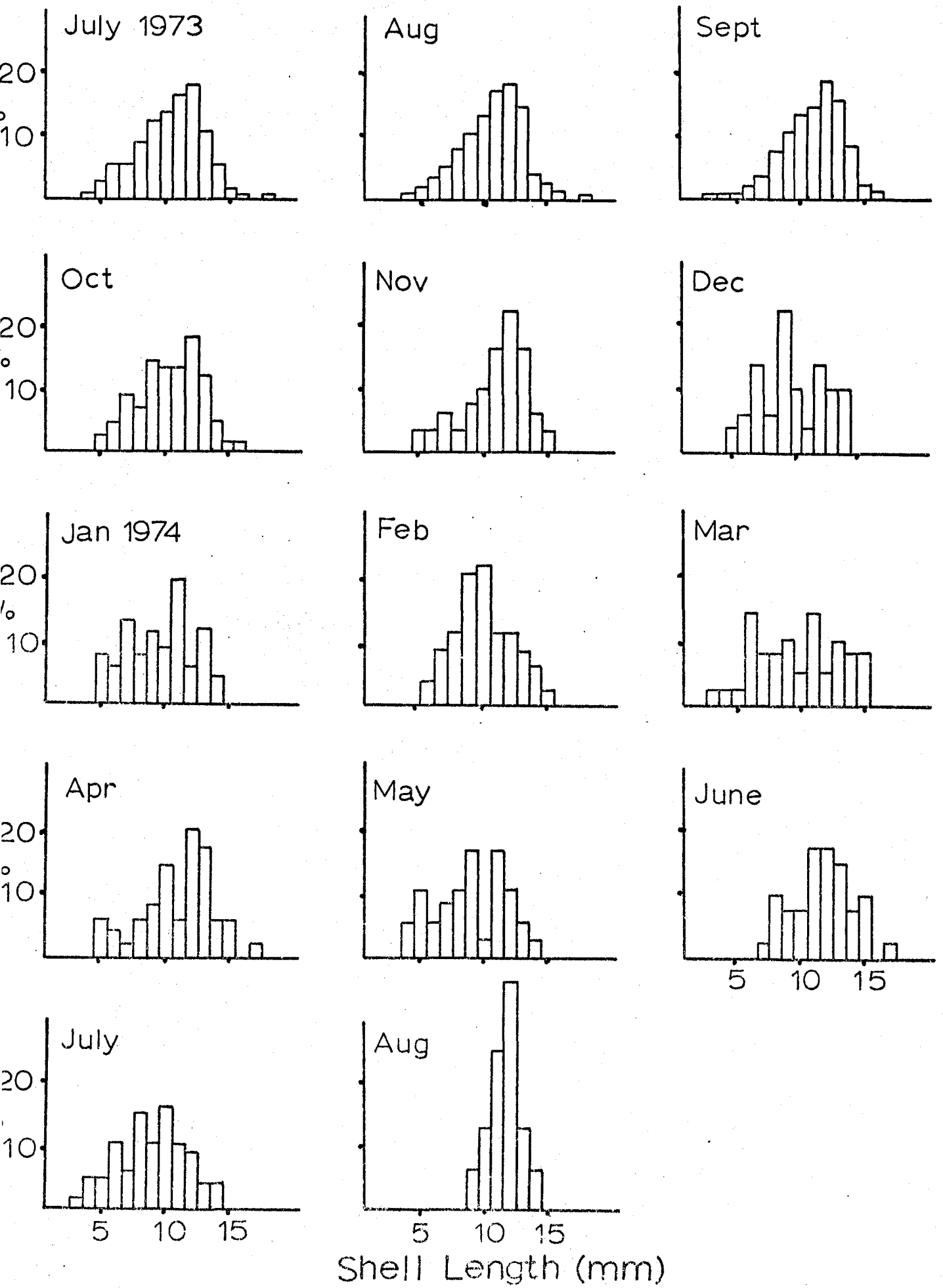

July 1973
Aug
Sept
Oct
Nov
Dec
Jan 1974
Feb
Mar
Apr
May
June
July
Aug
20
10
%
5
10
15
Shell Length (mm)

Figure 18. Size-frequency distributions of *Littorina planaxis* at Dillon Beach Site 2.

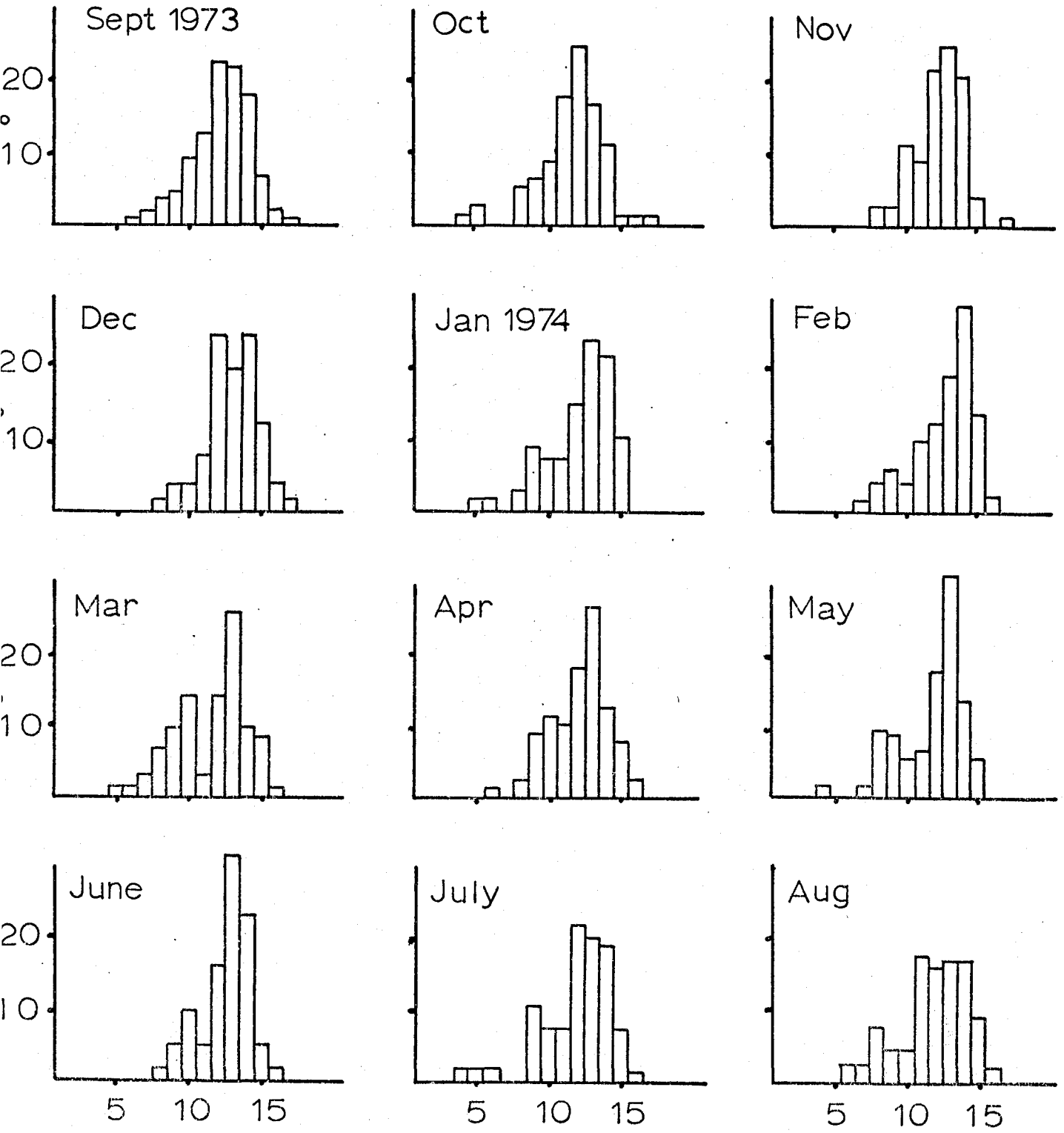

Sept 1973
Oct
Nov
Dec
Jan 1974
Feb
Mar
Apr
May
June
July
Aug
20
10
5
10
15
Shell Length (mm)

Figure 19. Size-frequency distributions of Littorina planaxis at Dillon Beach Site 3.

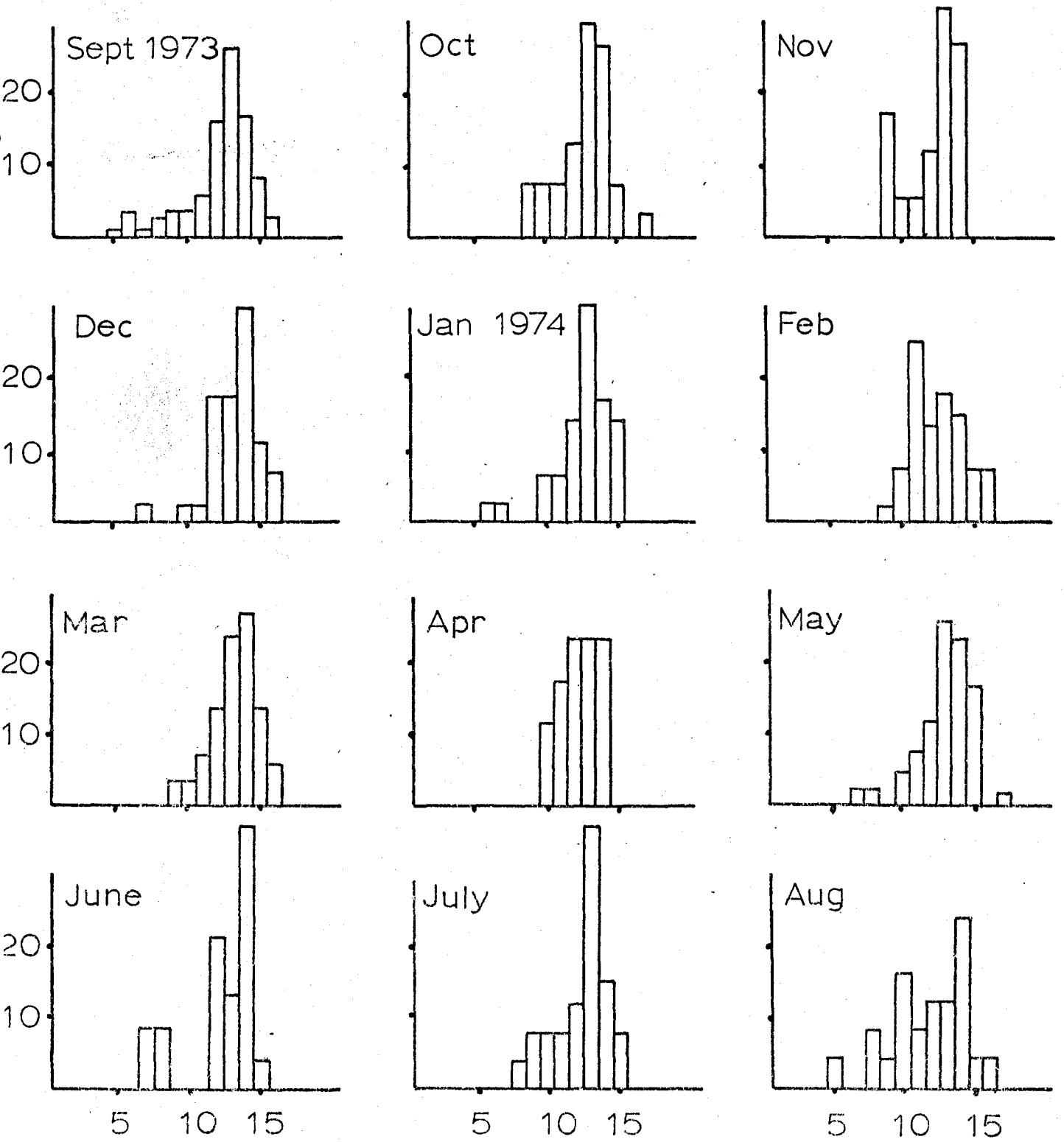

Sept 1973
Oct
Nov
Dec
Jan 1974
Feb
Mar
Apr
May
June
July
Aug
20
10
5
10
15
Shell Length (mm)

Figure 20. Size-frequency distributions of Littorina planaxis at Bodega Head Site 1.

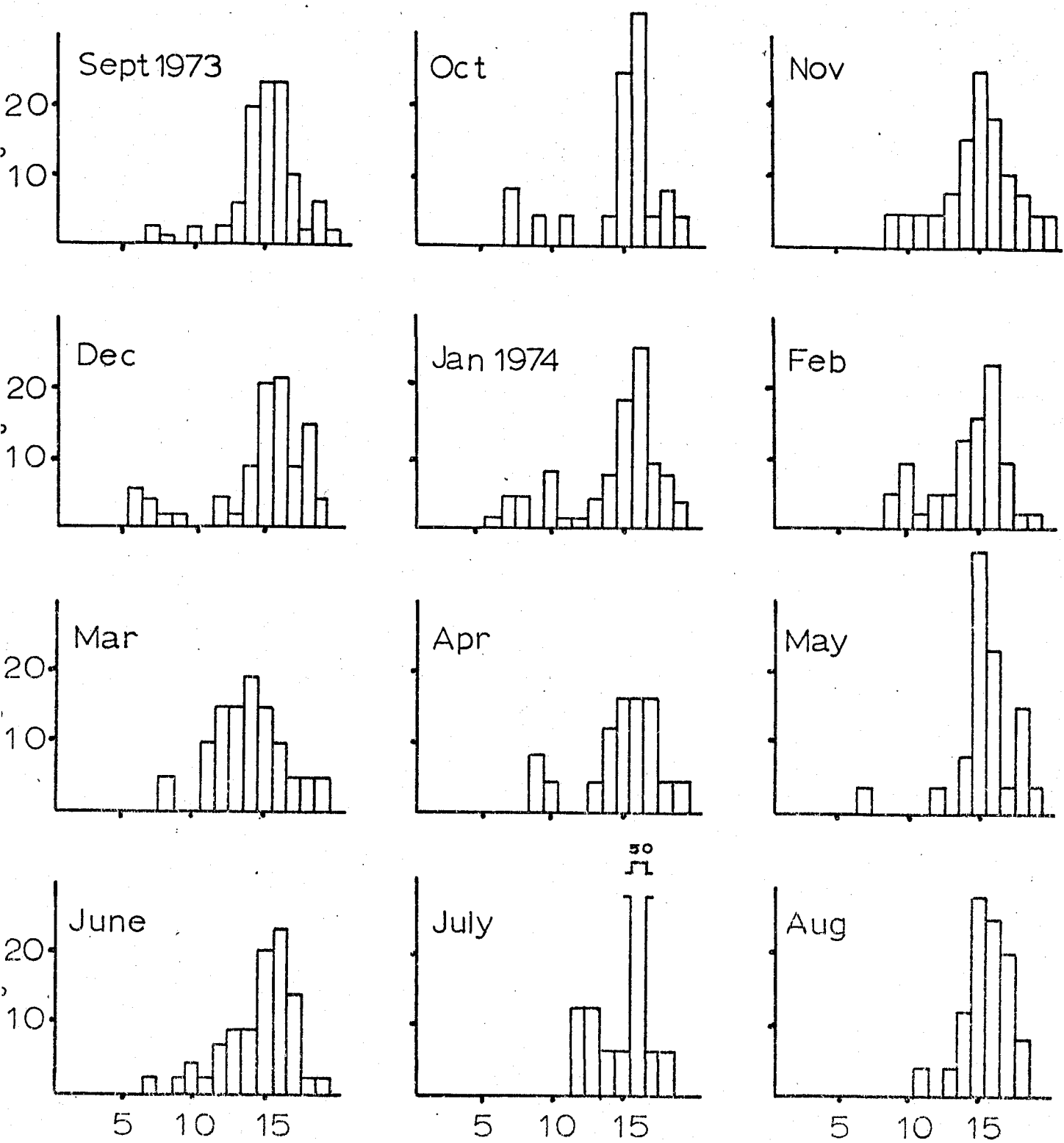

Sept 1973
Oct
Nov
Dec
Jan 1974
Feb
Mar
Apr
May
June
July
Aug
20
10
50
5
10
15
Shell Length (mm)

Figure 21. Size-frequency distributions of Littorina planaxis at Bodega Head Site 2.

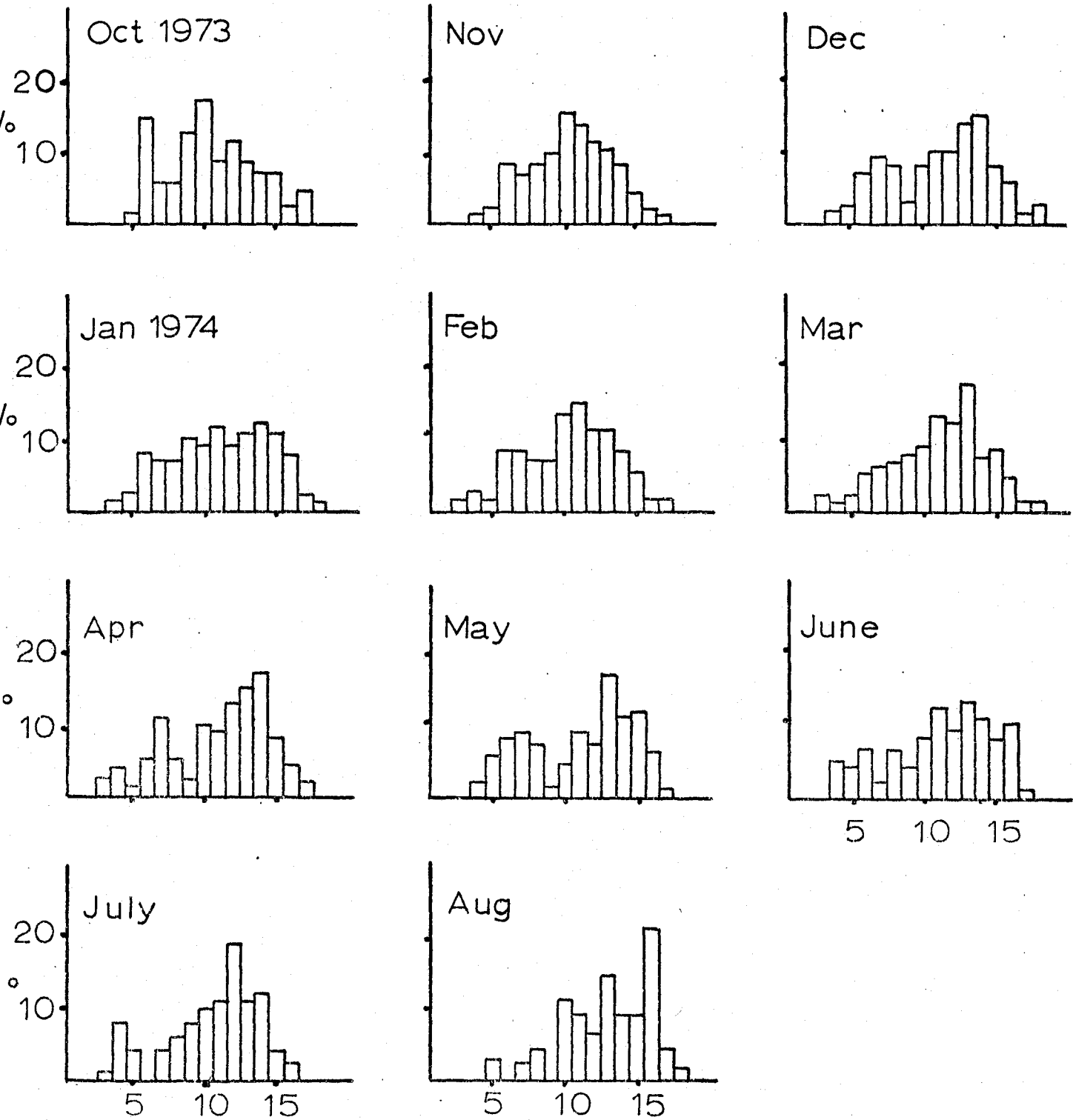
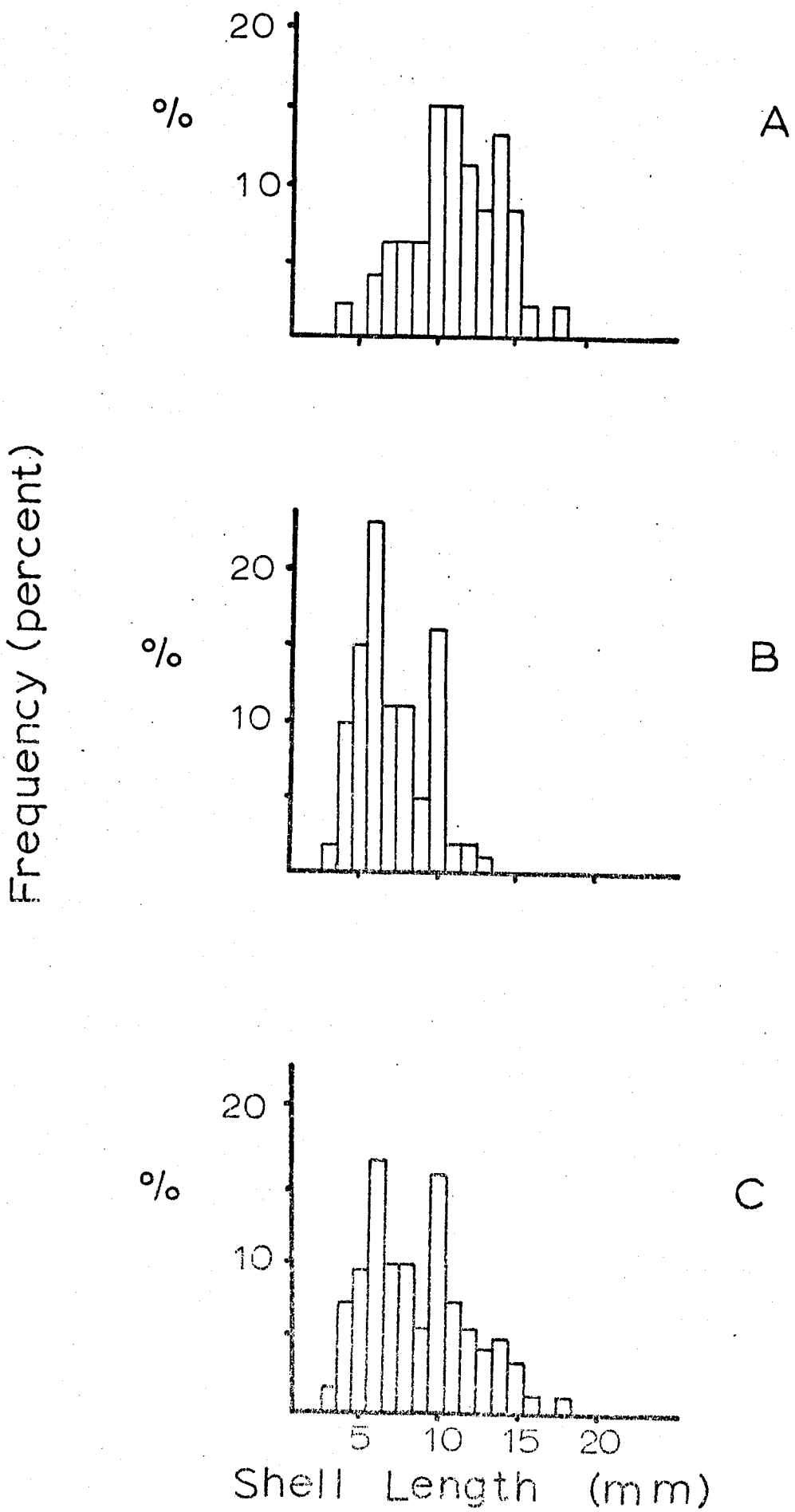

Oct 1973
Nov
Dec
Jan 1974
Feb
Mar
Apr
May
June
July
Aug
20
10
5
10
15
Shell Length (mm)

Figure 22. A. Size-frequency distribution of *Littorina planaxis* in control population of nursery.

B. Size-frequency distribution of *Littorina planaxis* in nursery section.

C. Size-frequency distribution of combined population.


Frequency (percent)
20
%
10
A
20
%
10
B
20
%
10
C
5
10
15
20
Shell Length (mm)

GROWTH

Methods

Changes in shell length (maximum shell height) were measured for individually marked snails from August 1973 to August 1974. A total of 575 snails from Dillon Beach Site 1 were collected and marked by writing sequential numbers on their shells with India ink. An additional 210 snails from Bodega Head Site 2 were marked in February 1974. The marking procedure involved inscribing two identical numbers directly on the snail shell which were then coated with either epoxy or Dekophane (Rona Pearl Corp., Bayonne, N. J.). Epoxy proved unsatisfactory, and all numbers showing wear were replaced during the first six month growth check in February 1974. Snails were kept in the laboratory from five to seven days during the initial marking procedure, but subsequent measurements were accomplished in 24 hours or less. Numbered snails at Dillon Beach were measured at six month intervals to investigate the effect of reproductive effort on rate of growth.

Results

A linear regression was fitted to the plot of net annual growth increment against initial shell size (Figure 23). The size-specific growth increments were highly correlated with initial length ($t=13.01$; $df.\infty$; $r=-.705$). Smaller Littorina planaxis grew much more rapidly than larger ones. This pattern of growth has been noted for many other gastropod species (Lysagth 1941; Frank 1965b; Laxton 1970;

Spight 1972, 1974), although Frank (op. cit.) concluded the growth relationship for Tegula funebralis was not linear; smallest snails grew somewhat slower than slightly larger ones.

The linear decline in growth observed for L. planaxis resulted in a size after which no growth occurred (L_a) of 16mm (Figure 23). This theoretical "average maximum size" growth parameter was consistent with field observations: largest L. planaxis at Dillon Beach Site 1 were 17mm. However, this size class was extremely rare, and individuals of this size did not grow during the study. Snails in other populations may reach 20mm in length (Bodega Head Site 1). This discrepancy between largest sizes could be the result of faster growth rates in populations with larger maximum size.

A conventional growth curve relating shell length to years of growth was plotted assuming larvae metamorphosed at 1mm (Figure 24). L. planaxis grows quite slowly and may live for many years. Snails grew to approximately 3mm the first year, needing two years to reach the 4.5 to 5mm size of sexual maturation. This species reproduces for many years.

Littorina planaxis continues to grow after reaching sexual maturity. The effect of breeding effort on rate of growth was investigated for marked individuals at Dillon Beach. L. planaxis reproduces from March to early August (see Reproduction section). Accordingly, growth increments were measured at six-month intervals corresponding to non-breeding (Aug. - March) and breeding (March - Aug.) seasons. A plot of seasonal growth increment against initial size revealed that growth

was substantially reduced during breeding season (Figure 25). Regression slopes were compared by covariance analysis. Results indicated highly significant differences in rate of growth between seasons (ANCOVA: F_s=19.99; df. 1,∞; $p<.001$). Mean increment of growth between breeding and non-breeding seasons were compared using covariance analysis techniques presented to Dixon and Massey (1957). Increment of growth differed significantly between seasons (ANCOVA: F_s=606.6; df. 1,∞; $p<.001$).

Snails at Bodega Head Site 2 also grew very little during the reproductive season. Comparison of regression slopes between populations at Dillon Beach and Bodega Head revealed significant differences in growth rates (ANCOVA: F_s=14.35; df. 1,∞; $p<.001$), but not statistical difference in regression means (ANCOVA: F_s=1.15; df. 1,∞). Male and females did not differ in growth pattern at any time.

Differences in growth rates have been noted for other littorinids. Individuals of the ovoviviparous species Littorina saxatilis were found to grow faster and mature earlier at higher shore levels in response to the more abundant food supply there (Berry 1961). Rate of growth in the ubiquitous species L. littorea also varied with intertidal position; members lower in the range grew faster (Hayes 1929). Fish (1972) noted that onset of sexual maturity occurred during the second winter in estuarine populations of L. littorea, while open coast individuals did not mature until the third year. Williams (1964) established that low temperatures and sexual maturation significantly depressed growth in L. littorea, producing seasonal variation in growth increments.

Figure 23. Annual growth increment (mm) as a function of initial size. Regression equation is $Y = -1.03X + 16.04$, $t = -13.01$, $df. = \infty$, and $r = -.705$. Average maximum size, L_a, was approximately 16mm (X intercept).

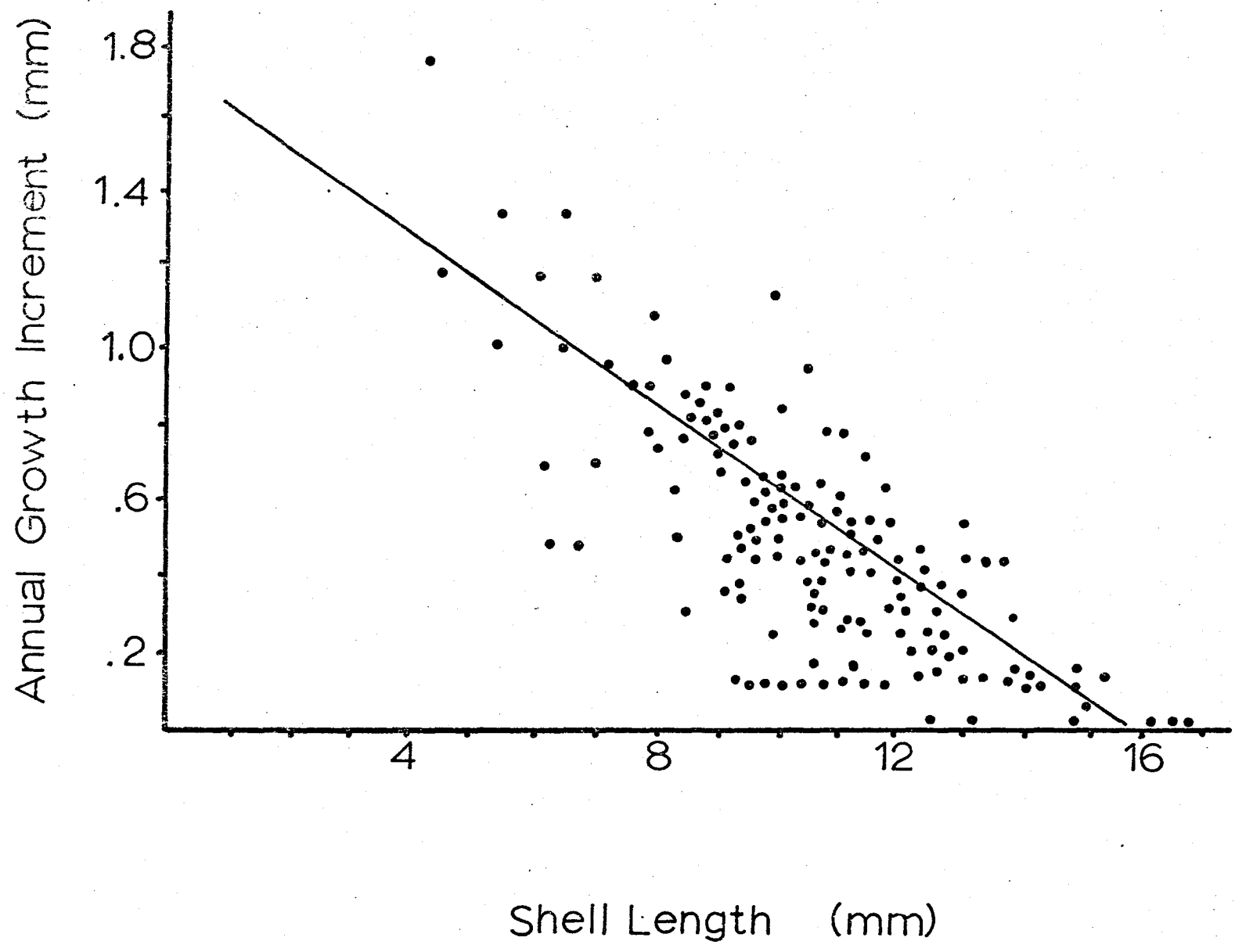

Annual Growth Increment (mm)
1.8
1.4
1.0
.6
.2
4
8
12
16
Shell Length (mm)

Figure 24. Idealized plot correlating shell length (mm) with age of snail (years). Size at metamorphosis was assumed to be 1 millimeter.

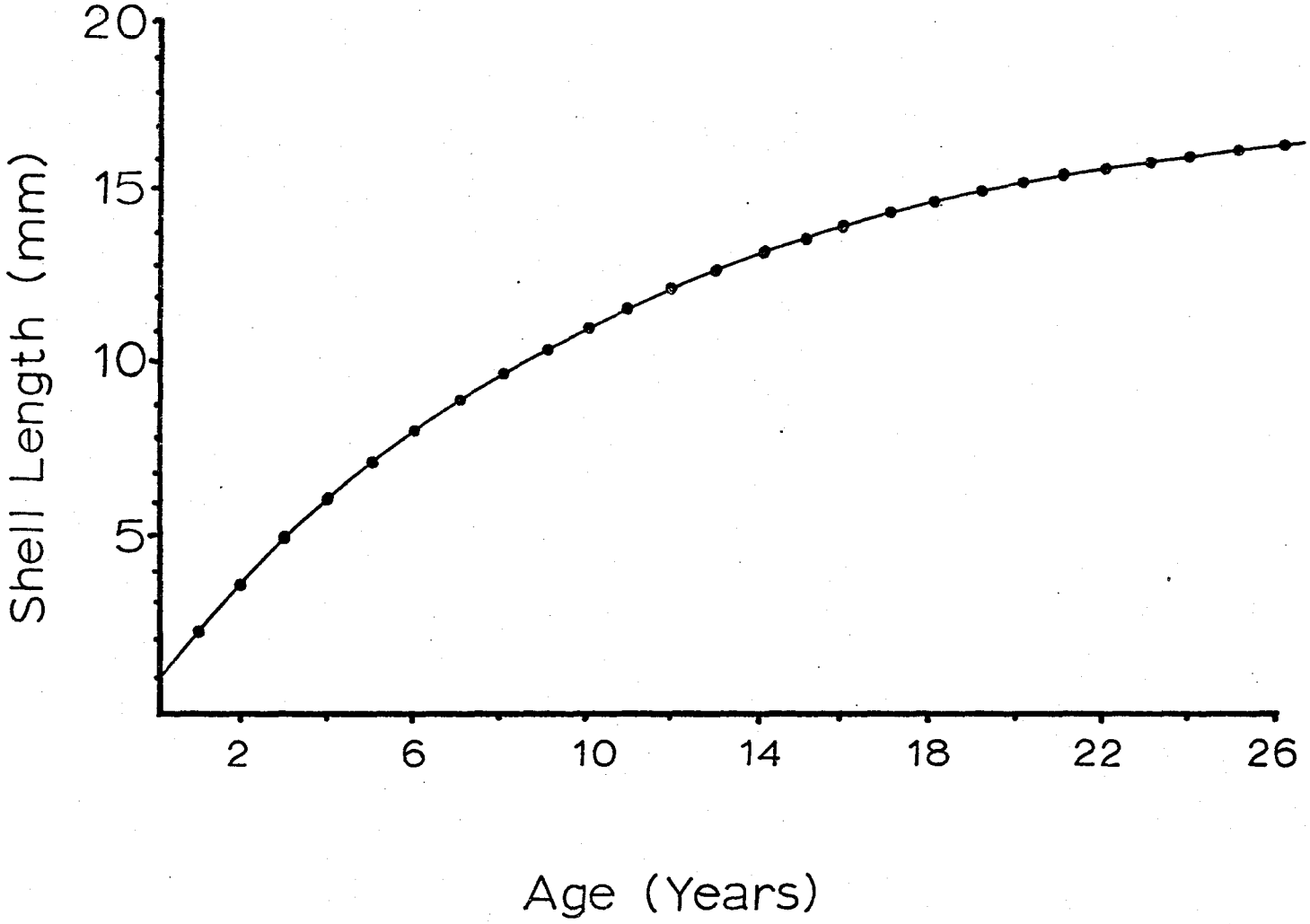
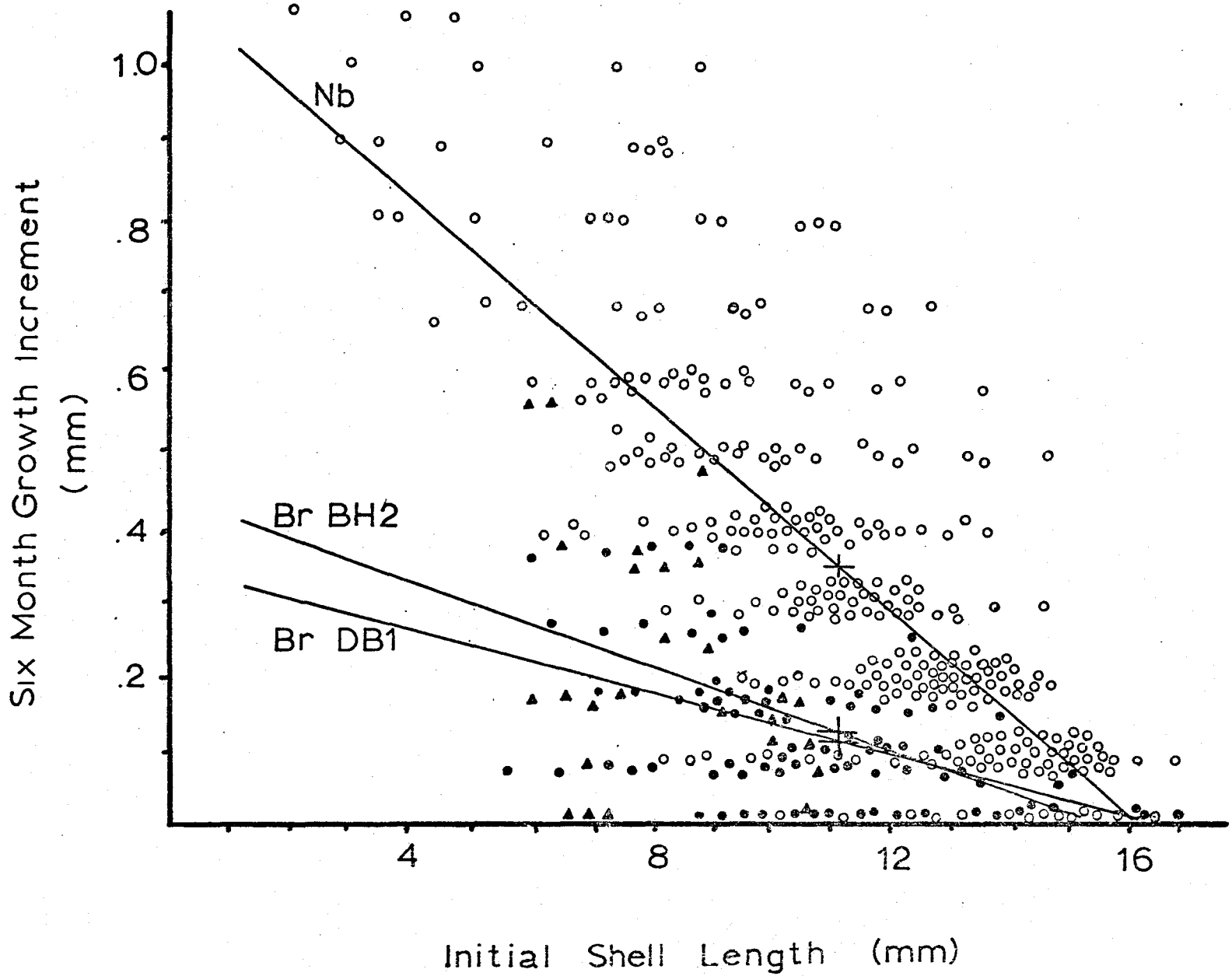

20
15
10
5
Shell Length (mm)
2
6
10
14
18
22
26
Age (Years)

Figure 25. Regressions for breeding (Br) and non-breeding (Nb) seasons. Equation for the non-breeding line was Y = -.642X + 10.67, ($\circ$) t = -11.24, df.∞, and r = -.516. Equation for Dillon Beach breeding ($\bullet$) snails was Y = -.194X + 3.29, t = -3.715, df.∞, and r = -.310. Equation for Bodega Head breeding snails was Y = -.269X + 4.33, t = -5.379, df.∞, and r = -.491. ($\blacktriangle$)


Six Month Growth Increment (mm)
1.0
.8
.6
.4
.2
Nb
Br BH2
Br DB1
4
8
12
16
Initial Shell Length (mm)

REPRODUCTION

Methods

Estimates of fecundity and breeding season were made using a spawning technique devised by Struhsaker (1966). Following collection from the field, snails were sexed and females placed in individual Stender dishes. The dishes were half filled with filtered sea-water (filter mesh 5u) and covered. Snails spawned if ready.

Fifty to one hundred females were collected at roughly two week intervals. Collections were more frequent during breeding season to establish lunar/tidal synchrony. Counts of spawning females were made the day following collection.

Fecundity was estimated using one hundred females of various sizes (range 7.5 to 17mm). Snails were prepared as described above, but were kept for 14 days (one-half of a lunar cycle). Initially eggs were counted daily; this frequency dropped with reduced egg production. Counting involved the following procedure: eggs were stirred into 30 milliliters of sea-water until a homogenous mixture was obtained. Two 1ml aliquots were drawn off and eggs counted using a Sedgwick-Rafter counting cell under a dissecting microscope. If the two counts were appreciably different, a third aliquot was counted. The mean number of eggs per aliquot were multiplied by 30mls to give the number of eggs spawned per female per spawning episode.

Copulation

Pairing behavior and subsequent copulation of Littorina planaxis has been described by Gibson (1964), and follows the general pattern discussed by Fretter and Graham (1962) for L. littorea. Copulating pairs of L. planaxis were observed in the field during every monthly sampling period except October and November 1973. Quantitative estimates were not made until breeding began, but less than one pair per square meter was noted from August 1973 to March 1974.

Extensive pairing commenced in March 1974 and ended in early August 1974. Data from Gibson (Ibid.) demonstrated maximum pairing occurred during the daily lower high tide. The percent number of snails copulating decreased with increasing wave shock (higher high tide) and when water was available (low tides). Struhsaker (1966) noted a similar pattern of activity for two Hawaiian species.

Using the daily lower high tide as a standard, an estimate of pairing frequency was made for one complete lunar cycle. The number of copulating snails in two one square meter quadrats were counted, and the total divided by the number of snails in the sample. The results, expressed as percent number of snails copulating, illustrates a marked semilunar pattern (Figure 26). Pilkington (1971) also noted this association, and attributed it to tidal height fluctuations.

Pilkington (Ibid.) and Struhsaker (1966) were unable to induce copulation of their study species in the laboratory. Littorina

planaxis would commence pairing and copulate in the laboratory when wetted. The field pattern of fluctuating number of snails copulating is probably associated with availability of water.

Size at Sexual Maturity

Females: Sexual maturity was established for females by gonadal smears and spawning experimentation. Shell length averaged between 5.5 to 6.0mm for size of female maturity. Smaller females did not spawn eggs, nor did their ovaries contain mature eggs. Mature females possessed much-enlarged reddish-brown ovaries with many mature pink eggs.

Males: Observed copulation and presence of a penis was used to estimate sexual maturation of males. Development of the penis was concomitant with onset of sexual maturity in two Hawaiian species (Struhsaker Ibid.). Males with a fully developed verge averaged 4.4 to 5.0mm. The smallest male seen copulating in the field was 5.0mm.

Sex Ratio

Gibson (1964) reported two males for every female in a breeding population of Littorina planaxis at Pacific Grove, California. A survey of 353 randomly chosen snails of various sizes at Dillon Beach in February, 1974, revealed 194 males and 159 females. No statistically significant difference from a 1:1 sex ratio was detected with a

chi-square test of frequencies.

Egg Capsules and Mass

Murray (In prep.) described the pelagic egg capsule of Littorina planaxis. The capsule typically contains a single ovum, although infrequently two and three ova have been noted within the same capsule. The shape of the capsule is remarkably similar to that produced by Littorina melanostoma, a Malayan mangrove species (see Berry and Chew 1973). The single ovum, measuring 90u in diameter, is surrounded by a symmetrical biconvex disc approximately 350 to 400u in diameter. The profile of the capsule is not symmetrical as depicted by Murray (op. cit.), but rather the edges are beveled (Figure 27).

The capsules are not shed directly into the sea, but are extruded from the female onto the rock substrate in a gelatinous sheath. Murray (op. cit.) also noted this structure, but termed it a gelatinous "ring". The sheath is elongated, coiled, and of varying length, but the ends are never continuous. Eggs within the structure are spiraled about the outside diameter (Figure 28). The sheath is not attached to the substrate, but is washed off the rock by wave action. The gelatinous material disintegrated within 22 to 24 hours after deposition in the laboratory, freeing the enclosed capsules.

Development

Development of Littorina planaxis within the pelagic capsule was typical of mesogastropods (Murray op. cit.). Veligers hatched into the plankton after six days at a size of 137u in diameter. Planktotrophic development is not known. Pilkington (1971) concluded that the planktonic lives of two New Zealand littorinids were quite long: 1-2 months. Williams (1964) estimated the pelagic stage of L. littorea to be 6-7 weeks. Size of L. planaxis at metamorphosis is not known, but Struhsaker (1966) reported 280-500u in shell length for the smallest post-veliger of L. picta and L. pintado. Murray (op. cit.) found L. scutulata began metamorphosis in the laboratory three weeks after hatching from the egg capsule. Settling L. scutulata were found to be 360u in diameter.

Spawning

Oviposition: Females that released eggs in the laboratory did not have one characteristic position. The snails spawned in any number of positions: exposed or submerged, oriented vertically or horizontally, or while moving or stopped. Other workers describe a typical position for several littorinid species. Female snails positioned themselves vertically at the air-water interface with the ovipositor submerged (Lenderking 1954; Struhsaker op. cit.; Berry and Chew 1973).

All workers agree that water is essential to induce spawning. Littorina planaxis would spawn once when placed in water, but agitating the dish or changing the water on a daily basis induced subsequent spawning. Struhsaker (op. cit.) noted a similar pattern for two pelagic capsule producing Hawaiian species, although water movement had to coincide with the appropriate phase of the tide.

Seasonality of Spawning: Though copulation was observed in most months (albeit in low frequency during winter), release of eggs was limited to five months: March through early August (Figure 29). Accordingly, data on number of eggs spawned also demonstrated this seasonality (Figure 30). With the exception of December 7 laboratory spawning experiment, eggs released in winter months were not embedded in the gelatinous mass. This release of low numbers of eggs probably represented residual spawn.

Onset of spawning did not correlate with increasing air and surf temperatures (Figures 1 & 2). Borkowski (1971) found gonads of six western Atlantic tropical littorinids to mature with warming air and water temperatures. However, spawning of these species was delayed nearly two months following gonadal maturation, suggesting that a critical temperature must be reached to induce spawning. Williams (1964) noted a similar maturation pattern in L. littorea populations at Craig-yr-Wylfa, Wales. Gonads ripened

during coldest months, and snails began spawning when air and sea temperatures rose. Buckland-Nicks et al. (1973) reported two peak periods of spawning in Littorina sitkana populations at San Juan Island, Washington. The biannual pattern correlated well with rate of change of day length, though the authors did not discuss the implications of a photoperiodic response.

Lunar/Tidal Synchrony of Spawning: Lunar periodicity was investigated by spawning fifty to one hundred snails at all phases of the moon. Snails used in the study were collected from the field on the day they were spawned, and returned the following day. Results indicate a marked semi-lunar rhythm of egg release (Figure 31). The pattern is interesting in that the frequency of spawning females increased at neap tide phases until the end of May, after which fewer snails spawned during inter-lunar phases. This pattern, and the maximal number of eggs released at this time, indicates that May and early June probably represents the maximum spawning effort for L. planaxis. It appears that fewer females released eggs during new moon spring tides than at full moon. Since tides were no higher at times of full moon, reasons for this difference are not obvious.

To establish whether Littorina planaxis has an endogenous

lunar rhythm of egg release or is dependent on a quantity of water available only during periods of spring tides, two experiments were conducted. In the first experiment, 100 female snails were placed in individual Stender dishes in an outdoor water-table. Water in the covered dishes was checked approximately every other day for egg capsules. Percent number of snails spawned and number of capsules produced were counted. The experiment began on the last quarter of the moon, and ran 14 days.

Results (Figure 32) indicate that Littorina planaxis can release eggs at all phases of the moon. 10% of the snails spawned by the second day, but 78% released eggs by the third day. This suggests that a minimum contact time with water is required to condition and induce spawning in L. planaxis. A large number of snails spawned during time of full moon, rendering this experiment somewhat inconclusive. The number of eggs dropped considerably shortly after the first few days (Figure 33), and may be attributed to the exhaustion of eggs or sperm. Snails used in this experiment were marked and returned to the field. Several were collected and placed in sea-water at weekly intervals until eggs were once again released. Two weeks after termination of the experiment, sample snails spawned when brought into the laboratory.

The second experiment was identical to the first except that it was initiated at full moon. The immediate spawning by all snails indicated that females were already conditioned (Figure 34).

Frequency of spawning females fell and averaged near 30% for the remaining 20 days of the experiment. It is interesting to note that a large percentage of snails released eggs two days following the new moon phase, but fewer than average spawned on the day of new moon.

Berry and Chew (1973) found tidal rhythmicity observed in field populations of Littorina melanostoma to break down during laboratory studies. However, this supralittoral species released eggs only during periods of full moon regardless of the time spent in water during experimentation. Borkowski (1971) concluded that littorinids do not have an endogenous lunar rhythm, but rather spawned facultatively when water was available. The continuous spawning by L. planaxis suggests that it does not have a true lunar rhythm.

Daily Tidal Rhythm of Spawning: Struhsaker (1966) found two Hawaiian species, Littorina pintado and L. picta, have a tidal periodicity: both species spawned at time of the daily highest high tide. Berry and Chew (op. cit.) did not observe this in L. melanostoma. Two laboratory experiments were conducted to investigate this aspect of spawning in L. planaxis.

The first experiment was run using fifty females placed in individual dishes. The experiment began during the full moon period of June 4-5, 1974. Snails were introduced to water at the time of predicted low tide in the field, and

observed every hour to count number of females spawned and number of masses released. Figure 35 shows that release of the first egg masses began two hours after contact with water. By the time of the highest daily tide, 98% of the females had spawned 96% of the total number of masses produced. From the second hour to the time of highest tide (four hours), the number of masses produced per hour remained fairly constant: 30-45/hour.

The second experiment was identical to the first except that the snails were placed in water at time of the day's higher spring tide. Figure 36 reveals that females did not spawn until the following higher tide, some 25 hours after initial contact with water. Again the snails began spawning four hours before time of high tide and had completed releasing eggs by time of high tide.

Release of eggs in the field was observed on two occasions. Approximately ten minutes after females were first wetted by splash of the incoming tide the first females began spawning. Wave splash reached the populations at most areas for approximately six hours during periods of spring tides. Spawning activity was not observed at actual time of highest tide, but snails were seen to release eggs as early as 3½ hours before high tide. On one occasion, a female was seen to deposit an egg mass 2½ hours after the daily highest tide. A cursory inspection of rock surfaces and tide pools following high tide failed to reveal any L. planaxis egg masses: apparently all had been swept away.

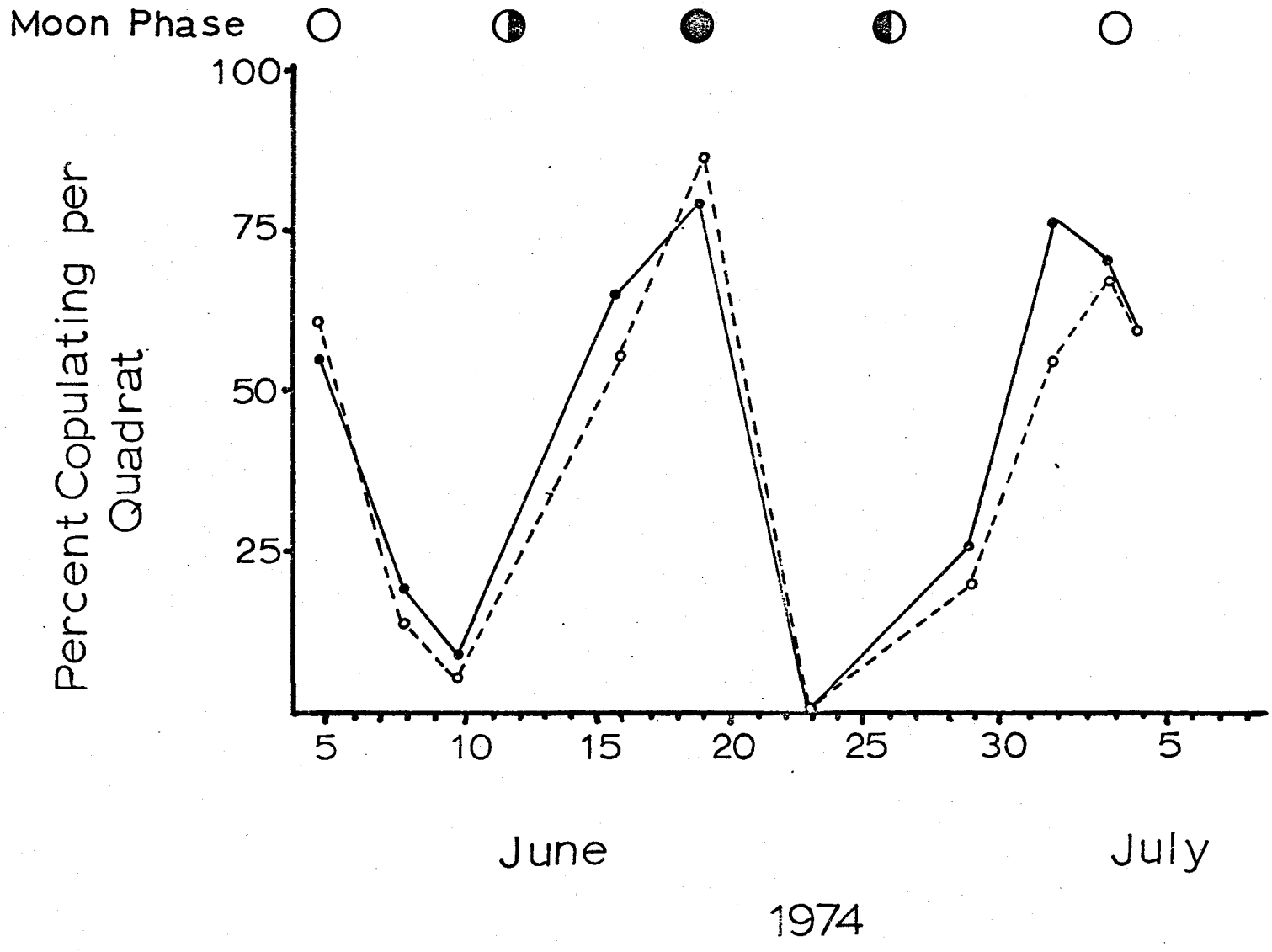
Size-specific Fecundities: The number of egg masses released by a female varied considerably within any size group. A large Littorina planaxis could produce five masses each with a moderate number of eggs, or one large mass containing several thousand capsules. Accordingly, the number of eggs spawned per female in a single spawning episode was used to estimate size-specific fecundities.

Data presented in Figure 37 represents the number of capsules produced by one hundred L. planaxis of varying sizes (range 7.5-17mm) in eight induced spawning episodes. The spawns were spread over a fourteen day period to encompass full and quarter moon phases. Dissections of ten randomly chosen snails at the end of the experiment showed that very few mature eggs were left in the ovaries.

It can be seen from Figure 37 that the number of eggs produces by a single female was enormous: 14,200 eggs on the average. The size-fecundity relationship was exponential. The larger number of capsules produced during the fecundity study probably represents maximum spawning of snails in natural populations. Field populations were not able to spawn continuously over any fourteen day period due to fluctuations in tidal height. Furthermore, differences in egg production during breeding season were ignored. However, disregarding these aspects, seasonal fecundity can be estimated by multiplying the number of eggs produced per female

in one lunar period by the number of lunar periods in a breeding season (approximately eight: Figure 30). Thus the yearly fecundity of a 13mm Littorina planaxis was 113,600 eggs.

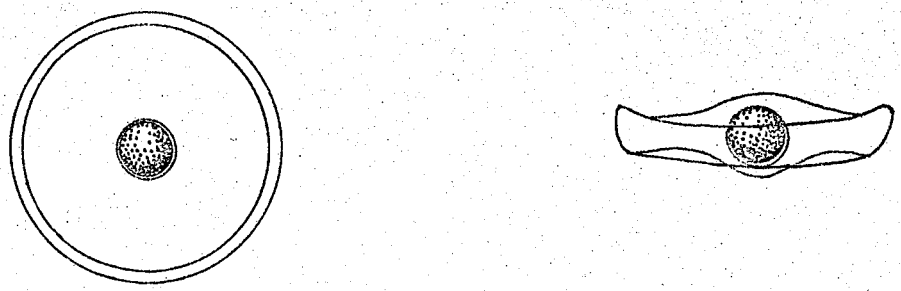
Figure 26. Pairing frequency of *Littorina planaxis* for one lunar cycle.


Moon Phase
100
75
50
25
Percent Copulating per Quadrat
5
10
15
20
25
30
5
June
July
1974

A. Top and side view of a Littorina planaxis egg capsule.

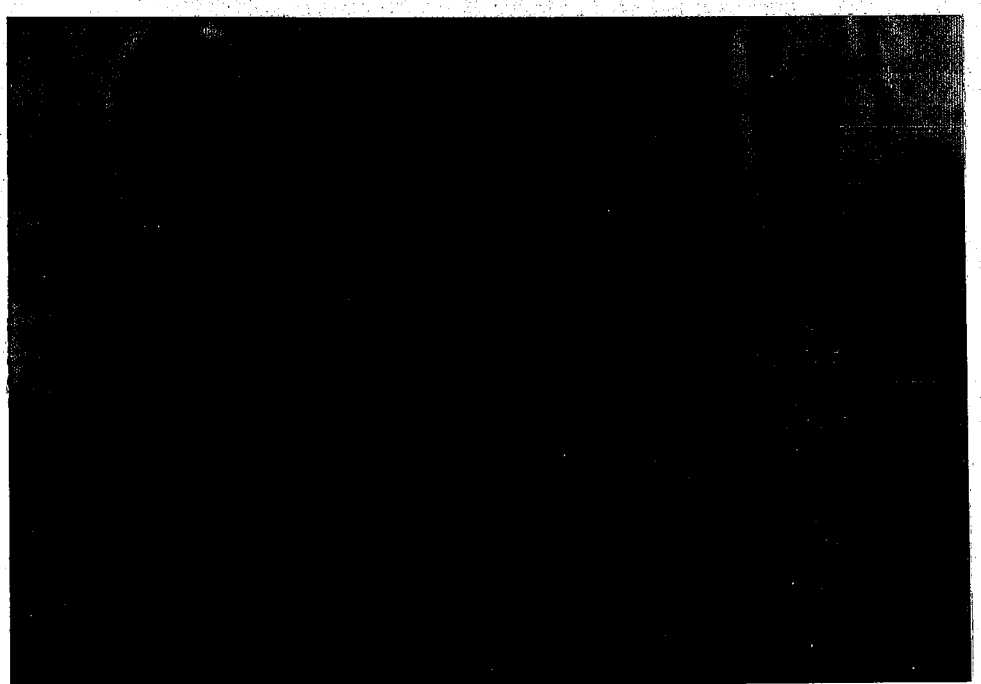
Figure 27.

B. Photograph of a Littorina planaxis egg capsule: side view.



100μ

100 μ

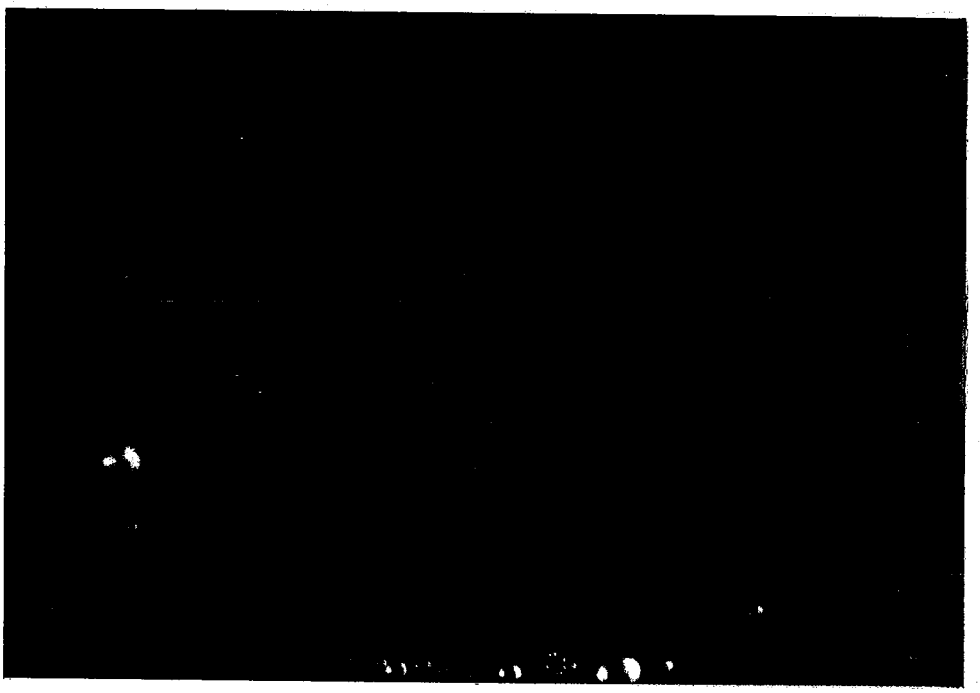


A. Photograph of Littorina planaxis egg mass containing several thousand egg capsules. Mass was approximately 12 millimeters in diameter.

Figure 28.

B. Photograph of the configuration of capsules within a Littorina planaxis egg mass. Eggs spiral around the outside diameter.

A



B

100μ

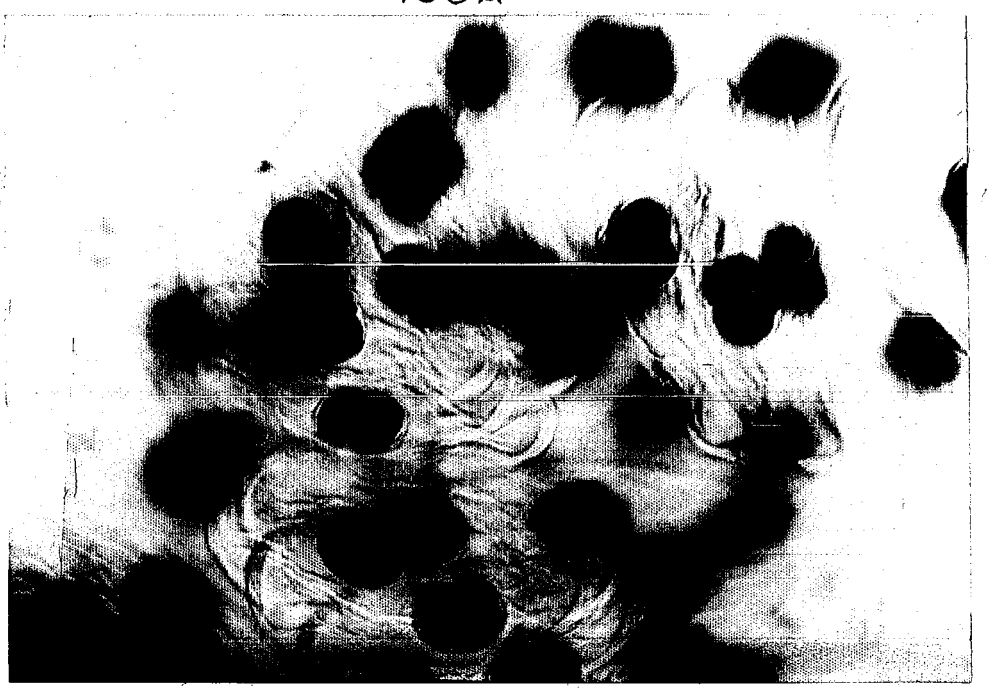


Figure 29. Breeding season for Littorina planaxis at Dillon Beach, Marin Co., California. The percent number of females spawning during full moon periods is shown.

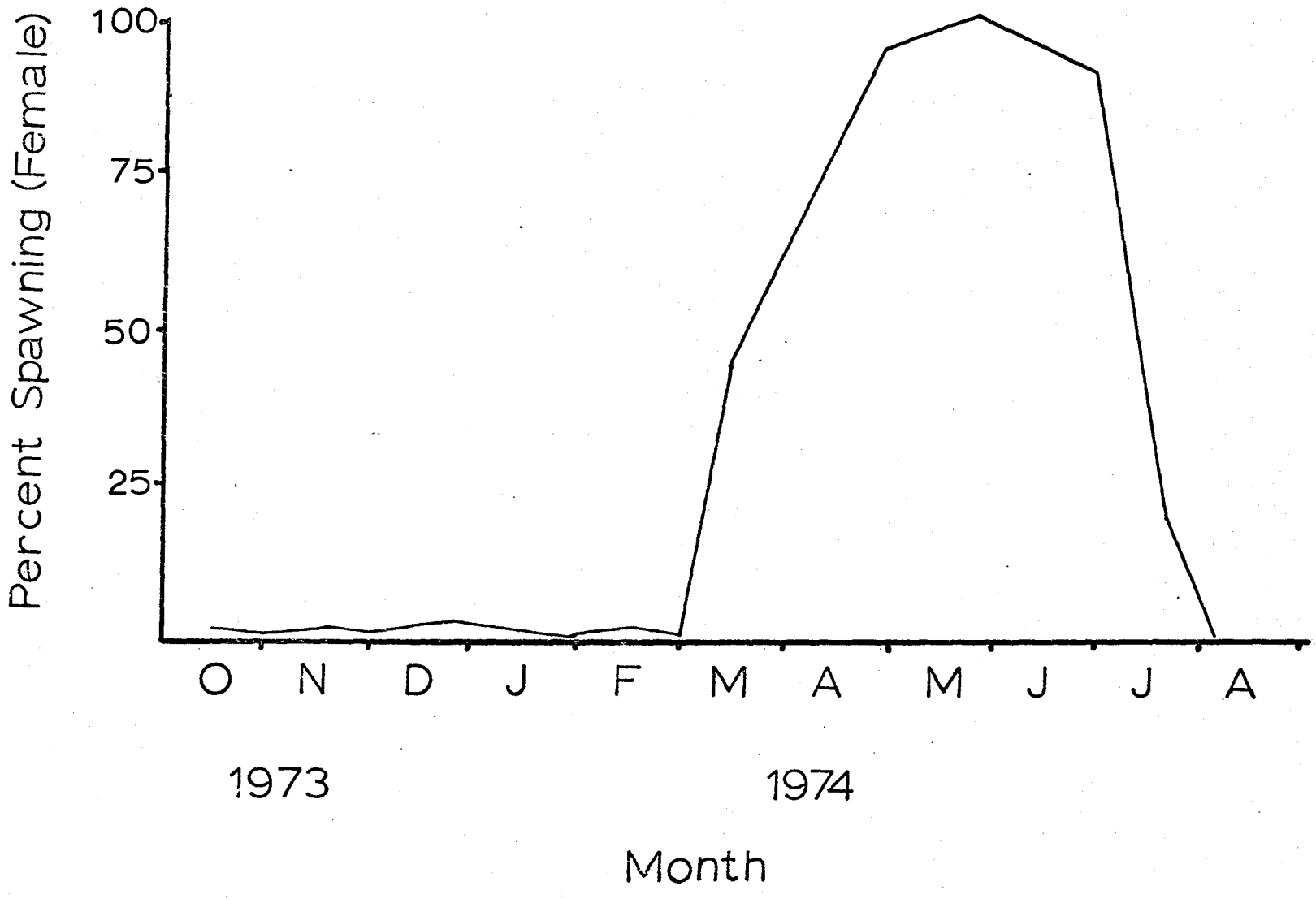

Percent Spawning (Female)
100
75
50
25
O
N
D
J
F
M
A
M
J
J
A
1973
1974
Month

Figure 30. Seasonality of eggs spawned by Littorina planaxis at Dillon Beach, Marin Co., California.

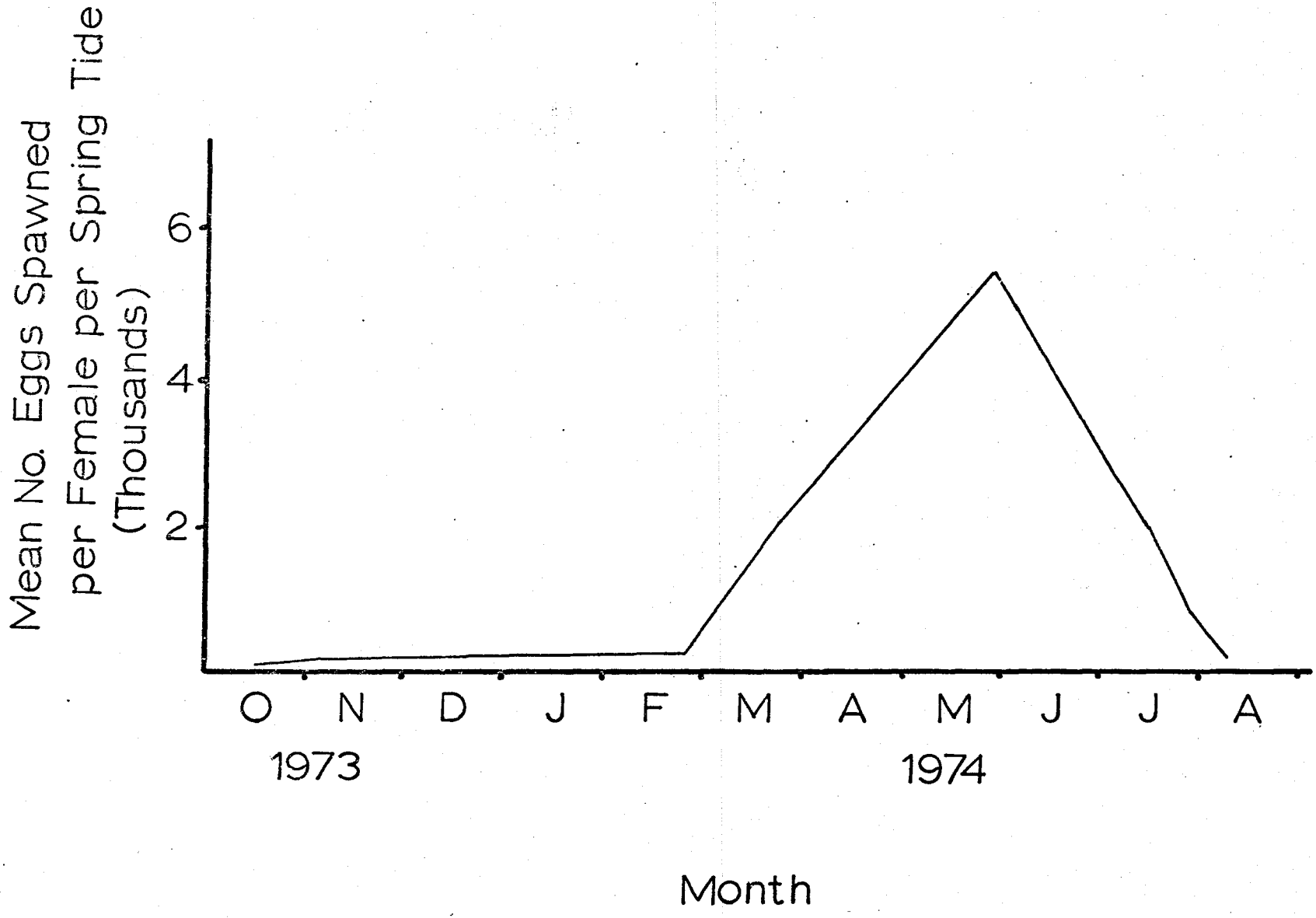

Mean No. Eggs Spawned per Female per Spring Tide (Thousands)
2
4
6
O
N
D
J
F
M
A
M
J
J
A
1973
1974
Month

Figure 31. Semilunar pattern of egg release in Littorina planaxis.

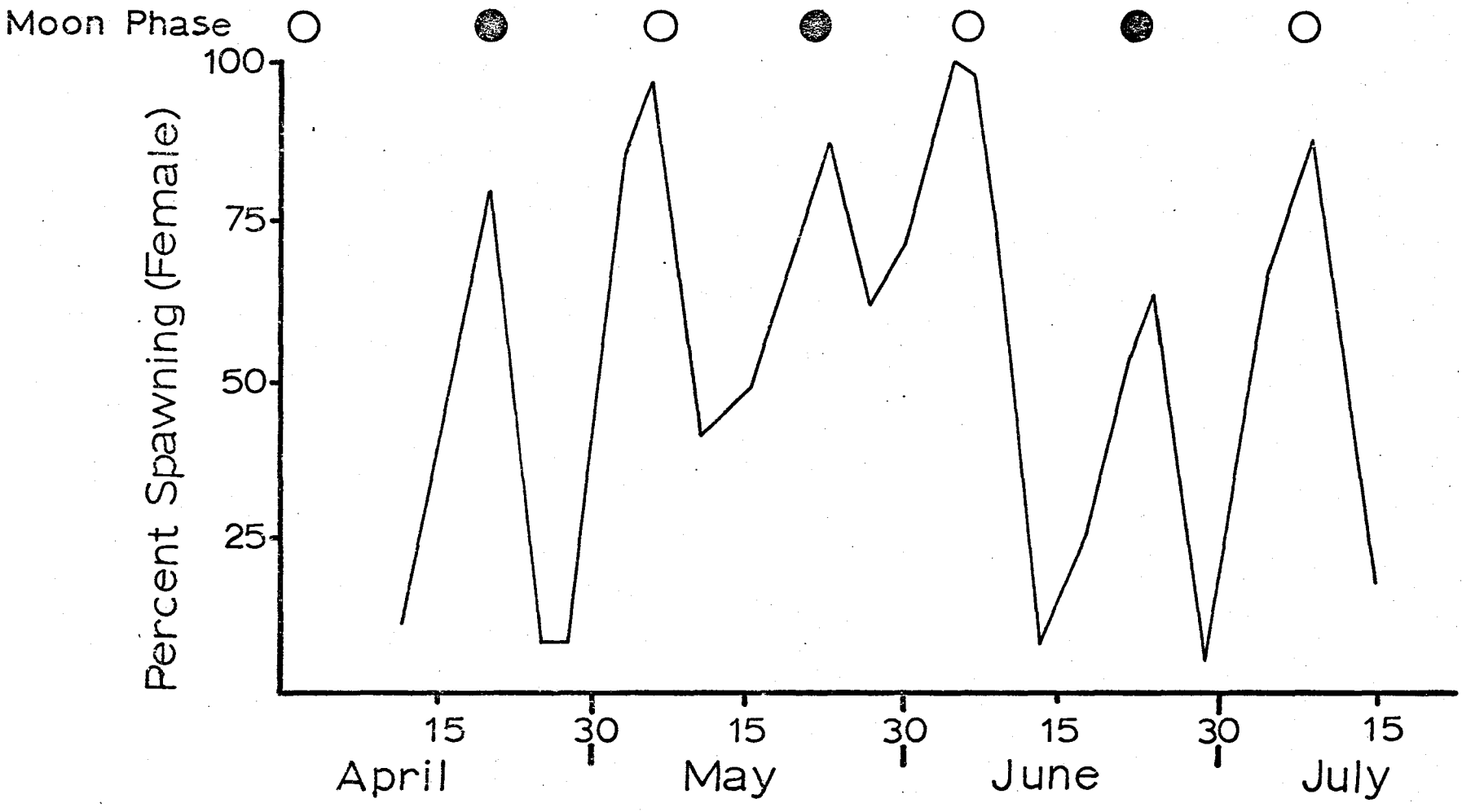

Moon Phase
Percent Spawning (Female)
100
75
50
25
15
30
15
30
15
30
15
April
May
June
July

Figure 32. Experiment 1. Percent number of snails spawning over a fourteen day period under natural photoperiods. Snails kept continuously in contact with sea-water.

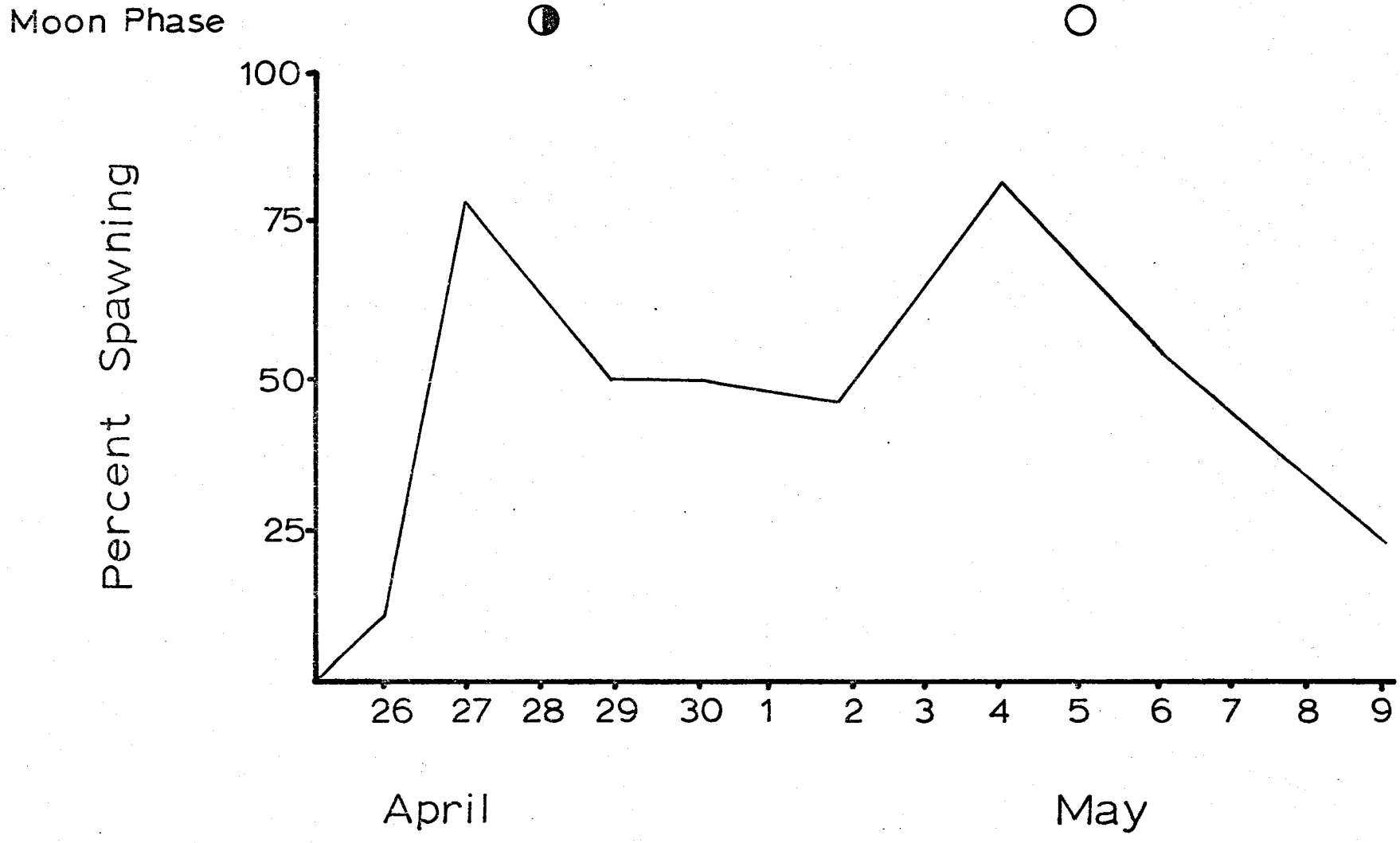

Moon Phase
Percent Spawning
100
75
50
25
26
27
28
29
30
1
2
3
4
5
6
7
8
9
April
May

Figure 33. Experiment 1. Number of eggs released by 100 snails over a fourteen day period. Snails kept continuously in contact with sea-water.

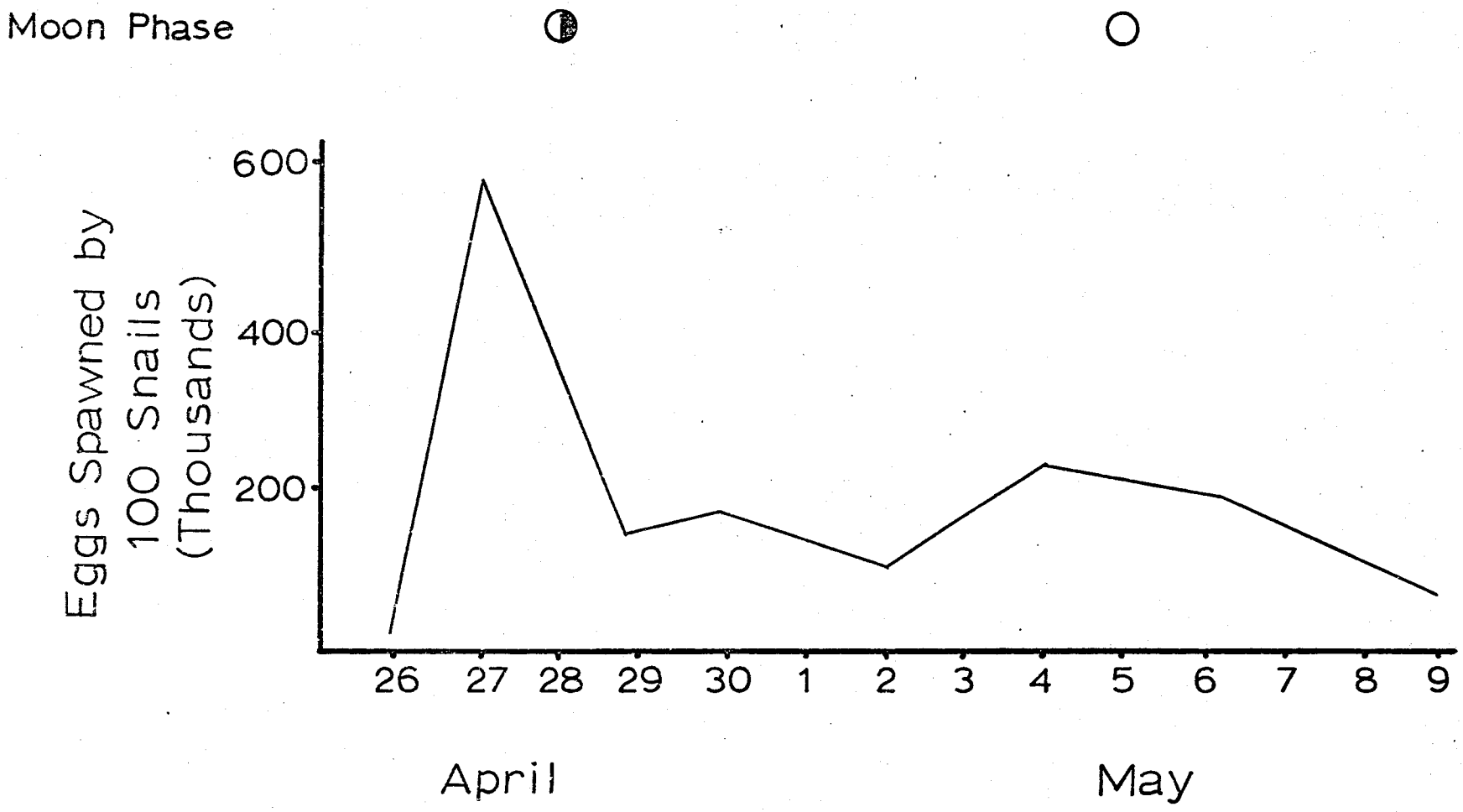
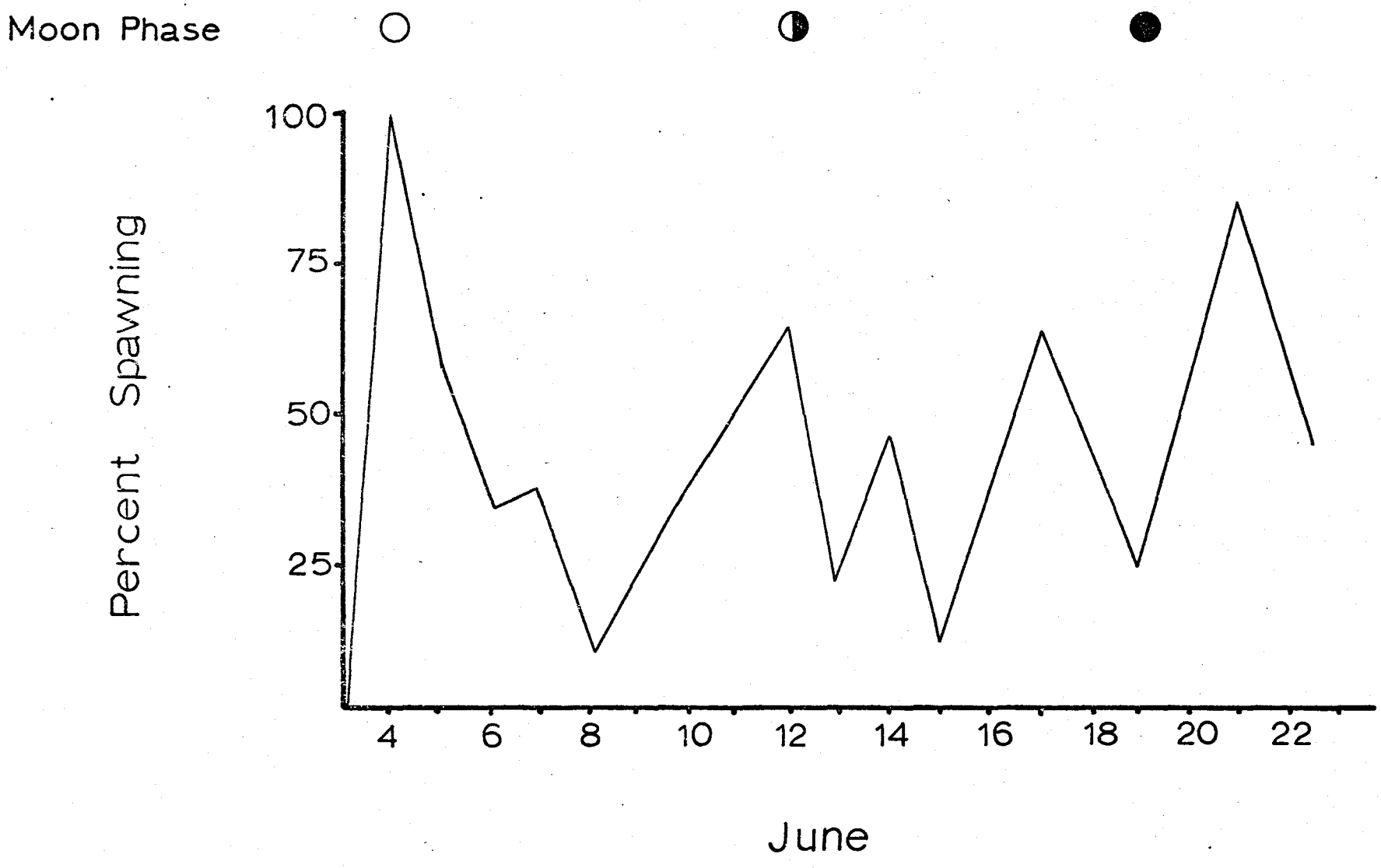

Moon Phase
Eggs Spawned by 100 Snails (Thousands)
600
400
200
26
27
28
29
30
1
2
3
4
5
6
7
8
9
April
May

Figure 34. Experiment 2. Percent number of snails spawning over a twenty day period under natural photoperiods. Snails kept continuously in contact with sea-water. Experiment began on day of full moon.


Moon Phase
Percent Spawning
100
75
50
25
4
6
8
10
12
14
16
18
20
22
June

A. Solid line represents the accumulative percent number of females that spawned, and the dashed line is the accumulative number of egg masses produced.

Figure 35. Daily rhythm of oviposition. Experiment 3 begun on daily lowest tide during full moon period.

B. Solid line represents the number of females that spawned per hour and the dashed line is the number of egg masses produced per hour.

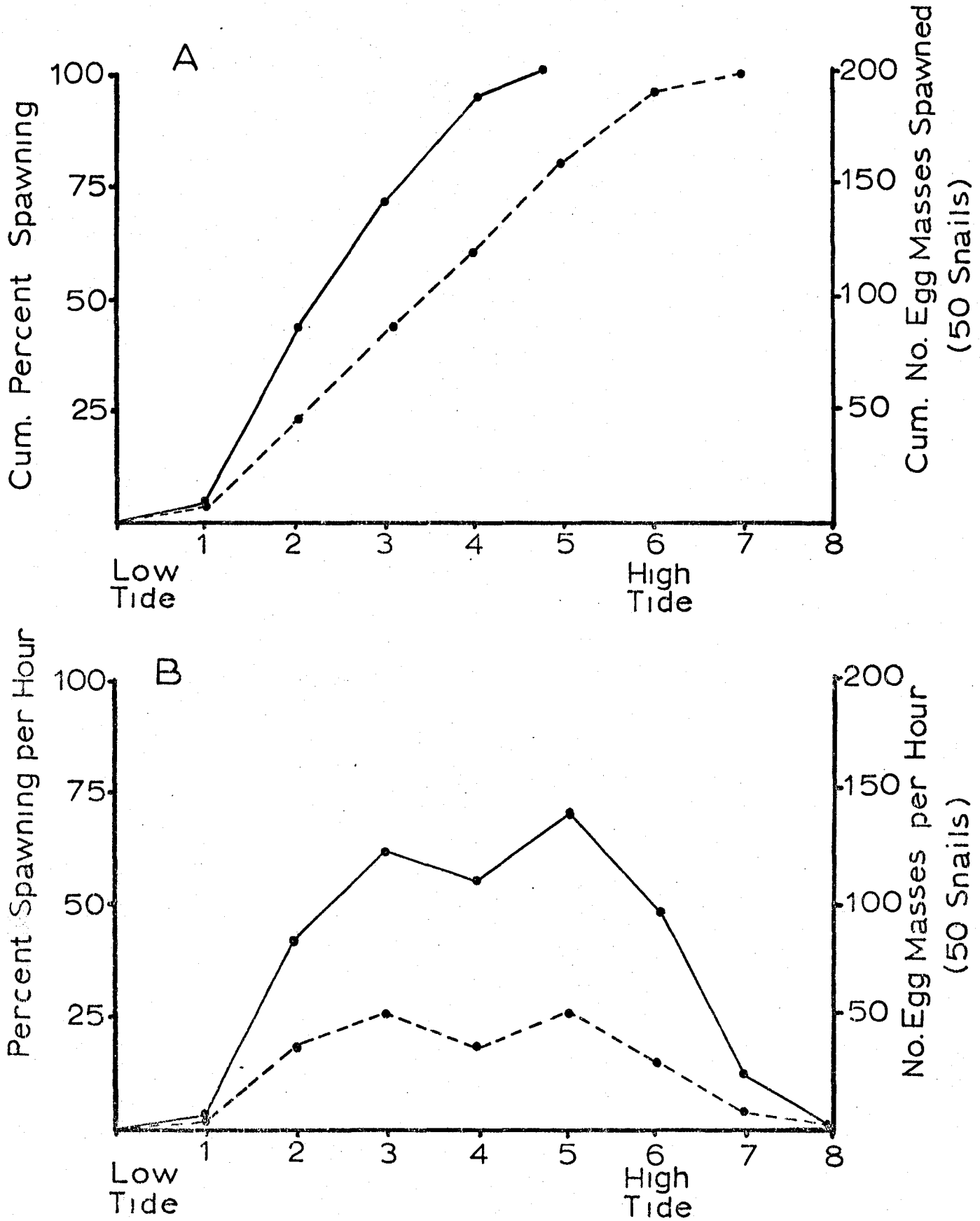

A
Cum. Percent Spawning
100
75
50
25
200
150
100
50
Cum. No. Egg Masses Spawned
(50 Snails)
1
2
3
4
5
6
7
8
Low
Tide
High
Tide
B
Percent Spawning per Hour
100
75
50
25
200
150
100
50
No. Egg Masses per Hour
(50 Snails)
1
2
3
4
5
6
7
8
Low
Tide
High
Tide
Hours Elasped From Immersion

Figure 36. Daily rhythm of oviposition. Experiment 4 begun at time of daily highest tide during full moon period. Dashed line represents the accumulative percent number of snails that spawned and the solid line the number of females that spawned per hour.

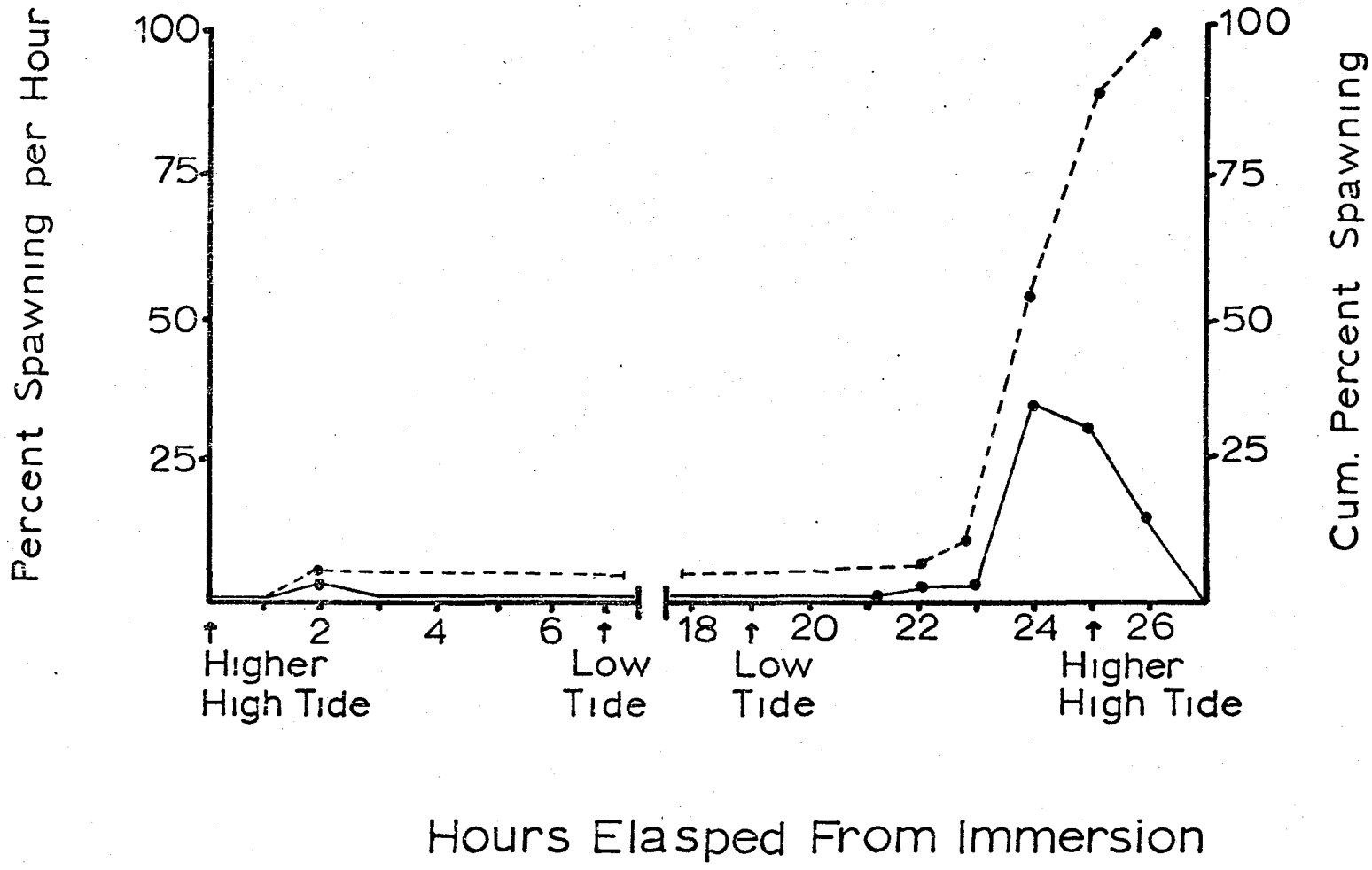
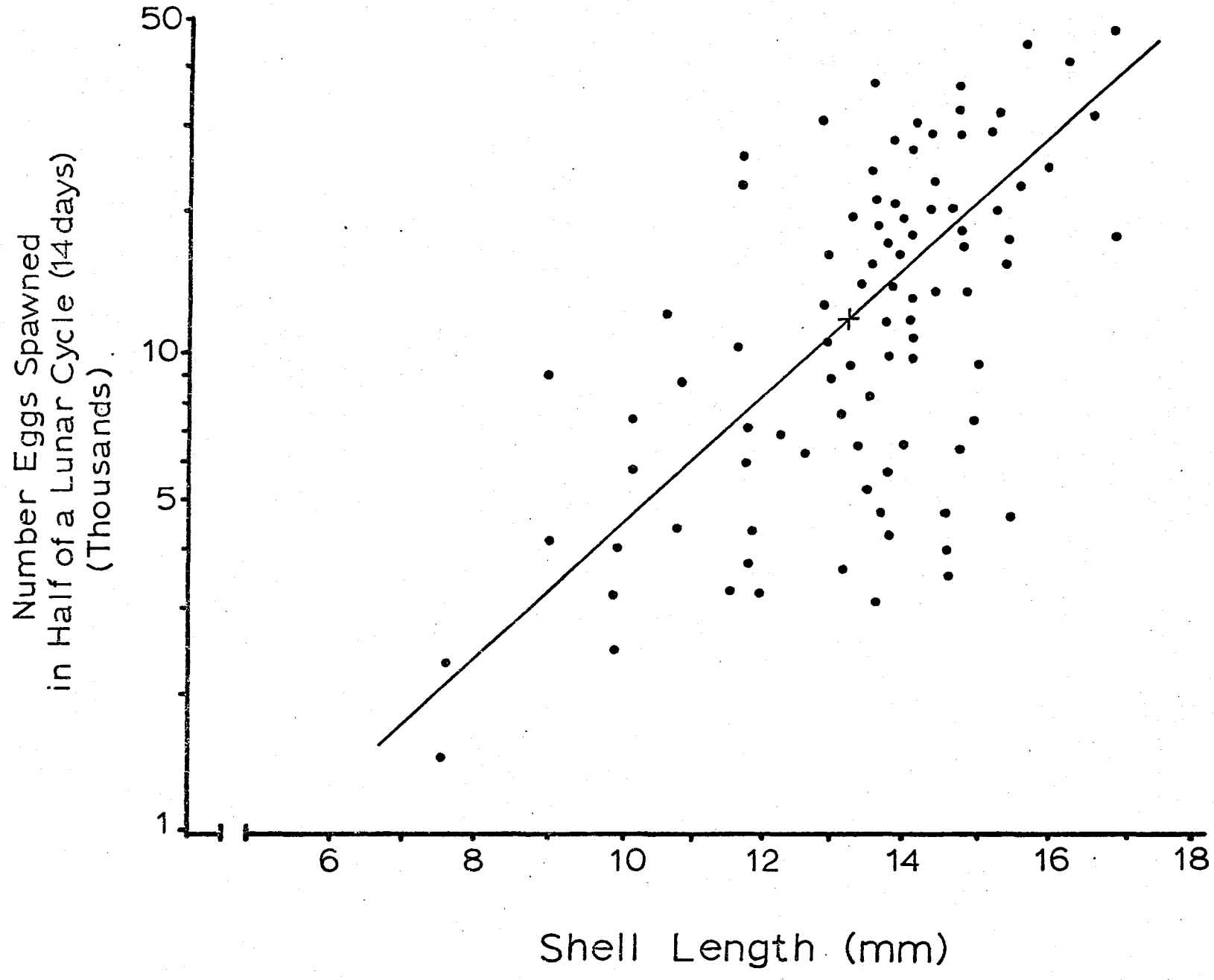

Percent Spawning per Hour
100
75
50
25
Cum. Percent Spawning
100
75
50
25
2
4
6
18
20
22
24
26
Higher High Tide
Low Tide
Low Tide
Higher High Tide
Hours Elasped From Immersion

Figure 37. Size-specific fecundities of Littorina planaxis. The regression equation is Ln Y = 13.35X + 5.058, t = 6.91, df. 100, and r = .5826.


Number Eggs Spawned
in Half of a Lunar Cycle (14 days)
(Thousands)
50
10
5
1
6
8
10
12
14
16
18
Shell Length (mm)

EVOLUTION OF REPRODUCTIVE STRATEGIES

An Initial Inquiry

The Littorinidae have three reproductive patterns, a greater number than is commonly found in any other prosobranch family. The patterns of this family are: 1) ovoviviparity, 2) direct development within benthic egg masses, and 3) pelagic egg capsules with planktotrophic veligers (Woodward 1909; Tattersall 1920; Kojima 1960). The vast majority of species produce planktotorophic veligers, though the Littorinidae are the only prosobranch family known to release pelagic egg capsules (Rosewater 1970; Pilkington 1971). Kojima (op. cit.) noted that the shape of the pelagic capsule varied, and he proposed the following classification: 1) drum, 2) simple drum, 3) helmet, and 4) disc. One variable not discussed previously is the number of ova per capsule. Other littorinid reproductive attributes vary. For example, some species breed all year while others have restricted breeding seasons. Large differences exist in the number of eggs released per spawning episode throughout the entire breeding season.

In view of the varying reproductive attributes of the Littorinidae, it would be interesting to investigate them in an evolutionary context. The purpose of this section is to

find out, with the limited data available, if correlations exist among the various life history features within the group. The second goal is to formulate initial hypotheses concerning the adaptive significance of the correlations. The study is restricted to considerations of adaptive strategies of littorinids because the group represents a morphologically conservative group inhabiting marine intertidal communities, but varying greatly in reproductive characteristics. Other groups of snails are not considered to avoid the complexity that would result from introducing the genetic and morphological diversity of taxonomically distant groups. Due to the limited data available on other genera of the family Littorinidae, only the genus Littorina is considered.

Complete demographic and reproductive information was not available for most species. For example, age and size at sexual maturity data were almost non-existent. Fecundities and number of eggs released per spawn were available for less than half the species listed. Tidal height occupied by a species varied on a population level due to differences in the physical make-up of the habitat (i.e., splash characteristics, topography). Therefore, generalized tidal levels, rather than actual heights, were used. Species in the littoral fringe were so designated, and those found lower than Mean Lower Low Water were placed in

a low intertidal category. Species found between these two extremes were considered mid- to high- intertidal forms.

Results

There is a highly significant correlation between size of the ovum and the number of ova released during a single spawning episode (Table 7). Many more smaller eggs were spawned than larger ones. Size of the ovum varied with type of development: planktotrophic eggs were significantly smaller than lecithotrophic eggs (Table 5).

Two types of pelagic egg capsules can be identified: capsules containing a single ovum and capsules with multiple numbers of eggs. Eggs within the multiple capsule were larger than eggs contained in single capsules. More eggs are spawned by species producing single eggs per capsule than by those releasing multiple egg capsules (Table 5).

A highly significant difference in the size of the ovum was found between littoral fringe species and species occupying other intertidal positions (Table 5). Littoral fringe snails spawned smaller eggs. A difference between number of eggs contained per capsule with intertidal position was also found. Fisher's Exact Test for Independence revealed a highly significant association between intertidal position and type of pelagic egg capsule produced (Table 6). Invariably, littoral

fringe species spawned egg capsules containing a single ovum. Species of mid-intertidal regions characteristically released pelagic capsules with multiple ova.

Type of development was found to vary with intertidal position. A significant association between direct/planktotrophic development and low/high intertidal positions was found (Table 6).

Temperate species were found to have larger ova than tropical relatives (Table 5). Tropical littorinids have egg capsules with a single ovum (Table 4 & 5). However, all tropical species are found in the littoral fringe, a region associated with species that characteristically produce pelagic egg capsules with a single egg.

Classification of Reproductive Strategies

Four generalized reproductive strategies associated with intertidal distribution can be described for Littorina:

1) Littoral fringe
   a. Oviparity
   b. Planktotrophic development
   c. Pelagic capsule with single ovum
   d. Small ovum
   e. High fecundity

2) High intertidal to littoral fringe
   a. Ovoviviparity
   b. Benthic juvenile
   c. Fecundity probably high

3) Mid- to high intertidal
   a. Oviparity

b. Planktotrophic development
c. Pelagic capsule with many ova
d. Larger ova
e. Less fecund

4) Low- to mid- intertidal
a. Oviparity
b. Direct development
c. Eggs embedded in benthic mass
d. Large ova
e. Low fecundity

Discussion

Woodward (1909) was the first to associate type of development with environmental habitat in Littorina. His scheme was as follows: littoral fringe species were viviparous (L. rudis (=saxatilis) and L. neritoides), littoral species were thought to have pelagic development (L. littorea), and low intertidal species were thought to reproduce by direct development (L. littoralis (=obtusata)). This association of developmental type with intertidal position was abrogated by the discovery of contradictory developmental modes. For example, Lebour (1935) discovered L. neritoides was oviparous, spawning pelagic capsules containing a single ovum. Struhsaker (1966) pointed out that the high intertidal position of L. scabra scabra, an ovoviviparous species, did not support Woodward's developmental scheme. More recently, Mileikovsky (1971) used the discrepancies in the classical Littorina developmental system to state that correlations between habitat and development types are not simple relationships.

A re-examination of the Littorina reproduction data indicates that a direct association exists between intertidal habitat and reproductive strategy. While development per se varies over the vertical range of the intertidal region, four identifiable suites of reproductive attributes are associated with intertidal position. Littoral fringe species invariably spawn pelagic egg capsules with a single small ovum. The planktotrophic veliger is subject to the

benefits of pelagic life (large and fairly constant food supply; constant environmental conditions) while suffering from inherent sources of mortality (predation; inability to find suitable settling sites). Littoral fringe populations may gain certain advantages by producing planktotrophic larvae. For instance, dispersion and recolonizing ability have long been recognized as potential benefits (Thorson 1946, 1950; Scheltema 1971; Mileikovsky 1971; Strathmann 1974; Spight ms). Eggs released in benthic masses in littoral and high intertidal levels would be subject to catastrophic mortality from physical conditions unless protected by substantial (and energetically costly) devices. Vance's (1973a) reproductive models predict that planktotrophic development would be favored when benthic mortality is greater than planktonic mortality, and if planktotrophic developmental time is not much longer than lecithotrophic development time.

An alternative to spawning pelagic egg capsules in high intertidal levels is to protect the young in brood sacs (ovoviviparity). This method has the advantage that recruitment into the population is constant. Though little data are available on the energetic cost of ovoviviparity in littorinids, there are indications that ovoviviparous species grow rapidly and have short life spans. Littorina saxatilis, an ovoviviparous species from the littoral fringe, reaches sexual maturity in 10 months at a

shell length of 7mm, and may live for three to four years (Berry 1961).

High to mid-intertidal littorinids also produce pelagic egg capsules, but with many ova within the same capsule. Additionally, the ova are larger than those spawned by littoral fringe species, and fewer eggs are released per spawn. The significance of placing many large eggs in a single capsule may not be immediately obvious, and, as yet, no single satisfactory theory exists. However, some data suggest that the strategies are again associated with intertidal position of the adult populations. Planktotrophic development would provide the same benefits for mid-intertidal species as for littoral fringe littorinids. However, if the length of feeding time in the plankton is dependent on egg size, mid-intertidal species that spawn larger eggs may have larvae with short pelagic lives relative to littoral fringe littorinids. If length of prefeeding time varies directly with egg size, mid-intertidal species should produce eggs that hatch from the capsule as veligers later than littoral fringe species, but perhaps at a larger size.

Data by Murray (In prep.) support these assumptions. Littorina scutulata, a mid- to high intertidal oviparous species, hatch as veligers eight days after release into the plankton within a pelagic capsule with many ova. The veliger was 169u in diameter at hatching. L. scutulata reached 360u and began metamorphosis

in three weeks. L. planaxis, a littoral fringe representative, hatched from the egg capsule in six days with a diameter of 137u. The duration of planktonic life is not known for L. planaxis, but Pilkington (1971) concluded that the pelagic lives of two New Zealand littoral fringe relatives were very long: one to two months.

If larger egg size ultimately provides a shorter planktonic existence, mid-intertidal species would have veligers subject to pelagic mortalities for less time than littoral fringe species. Pre-veligers of mid-intertidal littorinids are exposed to pelagic mortality for a longer time than littoral fringe species, but proportionately more mid-intertidal veligers may survive to metamorphosis due to the shorter total planktonic life span. Estimates of pelagic and juvenile mortality for L. planaxis is 99.99%, whereas far more L. scutulata and L. littorea larvae successfully metamorphose and reach sexual maturity.

The question remains as to why littoral fringe species release single eggs of smaller size. Time available to a pre-metamorphosis veliger probably varies with intertidal position of the adult population. Littoral fringe areas may be accessible only during periods of spring tides, while lower intertidal levels may be accessible during proportionately more tidal phases. Russell-Hunter et al. (1972) have shown that timing of settling in the littoral fringe salt marsh snail, Melampus bidentatus, is highly correlated with

spring tides. Post-veligers were seen to settle only during successive spring tides.

If pelagic development of littorinids with small eggs is longer than fourteen days, planktonic existence of littoral fringe species must last at least another fourteen days until the following spring tide. No littorinid with planktotrophic development is known to reach metamorphosis in two weeks, committing littoral fringe species to longer pelagic lives. Rapid development within the egg capsule by littoral fringe littorinids may be a consequence of small egg size, and long planktonic life may be due to both small size of the ovum and the inaccessibility of suitable settling sites.

The fourth reproductive strategy recognized for littorinids is direct development in benthic egg masses by species in the lower intertidal region. Recruitment problems, planktonic mortality, and possible benefits of pelagic dispersal are traded for constant recruitment with minimal wastage. Vance's (1973) model predicted benthic development when planktonic predation was greater than benthic predation, and when duration of development time in the plankton was long (i.e., short food supply). Relative to the littoral fringe, low intertidal areas represent more benign environments for larval development and subsequent juvenile survival. Since benthic egg mortality in the upper intertidal area would approach 100% without substantial egg protection, the alternative to planktotrophic development is ovoviviparity.

In summary, initial hypotheses concerning the adaptive significance of the life history correlations are:

1) High intertidal species must produce planktotrophic larvae, otherwise the energetic cost of benthic egg production is too high. Ovoviviparity achieves the same end by protecting the developing juvenile within the adult body.

2) High fecundities are imperative in situations where juvenile survival is low if adult population stability is to be maintained.

3) The significance of differences in numbers of eggs per pelagic capsule is not known, but it is suspected that it is related to conditions in the environment of the adult population as well as that of the larvae.

It is clear that environmental characteristics may preclude certain attributes without the evolution of less efficient or energetically costly modifications. The littorinids display many features that are desirable to test evolutionary theories of life history patterns. Information needed in this context concerns basic life history correlates of the individual (life span, growth, size and age at maturity) as well as data on reproduction in the group. Little data are available on energetics of eggs and capsules, growth and development of the planktotrophic larvae, and on the settling attributes of the metamorphosed larvae.

Perhaps the most important aspect in need of study is the effect of environmental conditions on juvenile survival. The present study supports Dayton's (1971) theory that community structure may be determined by environmental conditions of the adult habitat, not conditions in the plankton.

Table 4. Demographic and Reproductive Data on the Genus Littorina

Legend: tr= tropical, tm= temperate; lf= littoral fringe, hi= high, md= mid, lo= low intertidal; o= oviparous, v= ovoviviparous; d= direct, p= planktotrophic development; yr= year long, s= seasonal breeding.

Species	Climate	Tidal Position	Mean Size (Adult (mm)	Mean Size at Maturity (mm)	Age at Sexual Maturity (yrs.)	Mode Reproduc.	Develop ment	Breed Season	Mean Size of Ovum (um)	No. Eggs/ Spawn Episode	Fecundity (Annual)	No. Eggs/ Pelagic Capsule	Source
Subgenus Littorina													
planaxis	tm	lf	12	4	2-3	o	p	s	90	3720	113600	1	RJS
ziczac	tr	lf	14			o	p	s	75	4000	44000	1	4, 5
brevicula	tm	lf-hi	10			o	p	s	84			1	9
saxatilis	tm	lf-hi	10	7	1	v	-	s	-			-	2
scutulata type I	tm	md-hi	6	3		o	p		96	360		30	13, RJS
scutulata type II	tm	md-hi	6			o	p		100	560		5	6, 13, RJS
littorea	tm	lo-hi	18	11	2-3	o	p	s	205	500	15000	5	7, 16, 19
squalida	tm	lo-hi	24			o	p		95			14	8, 11
obtusata	tm	lo-md				o	d	s	205	230		-	16
sitkana	tm	lo-md		5		o	d	s	175	400		-	1, 6
atkana	tm	lo-hi				o	d		200	120		-	10
Subgenus Littoraria													
pintado	tr	lf	8	3		o	p	yr	60	3300	82000	1	15, 18
picta	tr	lf	6	3		o	p	yr	80	730	25000	1	15, 18
coccinea	tr	lf	19			o	p	s	90			1	14, 17
Subgenus Littorinopsis													
melanostoma	tr	lf	23	9		o	p	yr	60	4500	109000	1	3
irrorata	tr	lf				o	p						
scabra	tr	hi	30			v	-		-			-	15

Table 4. (Cont.)

Species	Climate	Tidal Position	Mean Size Adult (mm)	Mean Size at Maturity (mm)	Age at Sexual Maturity (yrs.)	Mode Reproduc.	Development	Breed Season	Mean Size of Ovum (um)	No. Eggs/ Spawn Episode	Fecundity (Annual)	No. Eggs/ Pelagic Capsule	Source
Subgenus Austrolittorina													
lineata	tr	lf	9			ö	p	s	75	1500	15000	1	4, 5
lineolata	tr	lf	13			o	p	s	120	900	12500	1	4, 5
undulata	tr	lf	19			o	p		90			1	14
Subgenus Melarhaphe													
neritoides	tm	lf				o	p	s	80			1	12

Sources for Table 4.

1 Behrens (1972)
2 Berry (1961)
3 Berry and Chew (1973)
4 Borkowski (1971)
5 Borkowski and Borkowski (1969)
6 Buckland-Nicks et al. (1973)
7 Fish (1972)
8 Habe (1958)
9 Kojima (1957)
10 Kojima (1958a)
11 Kojima (1958b)
12 Lebour (1957)
13 Murray (In prep.)
14 Rosewater (1970)
15 Struhsaker (1966)
16 Thorson (1946)
17 Vermeij (1972)
18 Whipple (1965)
19 Williams (1964)

Table 5. Two-way comparisons of *Littorina* data using Student's t-Test. (* = .05, ** = .01, *** = .001 probability)

	Mean	Variance	Student's t value	Degr of Free
Shell Length of Adult Female (mm)				
Temperate	12.29	43.238	-0.9182	15
Tropical	15.67	61.000		
Littoral Fringe	13.00	28.200	-0.5402	17
High-low Intertidal	14.86	87.809		
Oviparous	13.36	39.632	-1.2300	15
Ovoviviparous	20.00	200.000		
Shell Size at Sexual Maturity (mm)				
Temperate	6.00	10.000	0.4193	7
Tropical	5.00	12.000		
Single egg/capsule	4.75	8.250	-0.3269	6
Multiple eggs/capsule	5.67	21.333		
Number of Eggs per Spawning Episode				
Temperate	904.29	1620195.238	-1.9562	12
Tropical	2488.33	2716416.666		
Restricted breeding	1607.14	2546823.809	-1.0635	9
Year-round breeding	2843.33	3709633.333		
Single egg/capsule	2664.29	2480395.238	2.3262*	9
Multiple eggs/capsule	473.33	10533.333		
Number of Eggs per Pelagic Capsule				
Temperate	8.14	114.143	1.9015	14
Tropical	1.00	0.000		
Restricted breeding	1.50	2.000	0.3333	10
Year-round breeding	1.00	0.000		
Littoral Fringe	1.00	0.000	-6.1375***	14
High-low Intertidal	10.00	27.333		

Table 5. (Cont.)

	Mean	Variance	Student's t value	Degrees of Freedom
Mean Size of the Ovum (um)				
Temperate	133.00	3064.667	2.5104*	17
Tropical	81.25	367.756		
Direct Development	250.00	19900.000	4.1720***	17
Planktotrophic Dev.	93.33	1186.095		
Restricted breeding	119.90	2913.433	1.6480	12
Year-round breeding	66.67	133.333		
Single egg/capsule	82.18	271.364	-2.6909*	13
Multiple eggs/capsule	133.67	2820.333		
Littoral Fringe	82.18	271.364	-4.1605***	17
High-low Intertidal	153.71	2919.905		

Table 6. Degree of Association between Reproductive and Demographic data: Fisher's Exact Test for Independence. (* =.05, ** =.01, *** =.001 probability)

	Contingency Table		Probability
	Oviparous	Ovoviviparous	
Temperate	10	1	P = .99
Tropical	9	1	
Littoral Fringe	11	1	P = .99
Hi-Low Intertidal	7	1	
	Direct Development	Planktotrophic Development	
Temperate	3	7	P = .25
Tropical	0	9	
Littoral Fringe-High	0	14	P = .021*
Mid- Low Intertidal	3	2	
	Single egg / Pelagic Capsule	Multiple eggs / Pelagic Capsule	
Temperate	3	4	P = .05*
Tropical	8	0	
Littoral Fringe	11	0	P = .001***
Hi- Low Intertidal	0	4	

Table 7. Correlation coefficients for paried variable comparisons. (* =.05, ** =.01, *** =.001 probability levels)

Variable	Correlation Coefficient	Student's t value	Sample size
Length of Adult Female (mm) No. eggs released per spawning episode	0.5128	1.689	10
Length of Adult Female (mm) Mean Size of the Ovum (um)	0.1855	0.6262	13
Size at Sexual Maturity (mm) No. eggs released per spawning episode	0.0760	0.1704	7
Mean Size of the Ovum (um) No. eggs released per spawning episode	-0.6754	-3.0372**	13
Length of Adult Female (mm) No. eggs per pelagic capsule	-0.1287	-0.4497	14
Mean Size of the Ovum (um) No. eggs per pelagic capsule	0.1984	0.7300	15

DISCUSSION

Life history patterns are the result of natural selection (Cole 1954). Environmental characteristics represent strong selective forces influencing the allocation of an organism's time and energy among the biological processes (Slobodkin and Sanders 1969; Gadgil and Bossert 1970; Pianka 1970). Unusual life histories have been viewed as the result of extraordinary environmental requirements (Cole op. cit.). Often these unusual patterns represent end points on a continuum; one extreme is characterized by investment of most energy into reproduction, and the other by investment of most energy into growth and maintenance.

In an environment where exploited resources suddenly become available, organisms that emphasize reproduction are initially selected. However, the propensity to increase the efficiency of resource utilization by organisms characterized by high maintenance and growth attributes are subsequently selected as these organisms are capable of making fine adaptations to the local environment. These differences are exemplified by r- and K- reproductive strategies (MacArthur and Wilson 1967). Pianka (1970) listed correlates of these strategies. Briefly, the r- strategist is typically associated with uncertain or unpredictable climates. Mortalities in these areas are often catastrophic and density-independent, resulting in numerous episodes of recolonization. The consequences of rapid development,

small size, and early age of first reproduction is a high potential rate of population growth. K- strategists are characteristically inhabitants of predictable environments where mortality is density-dependent. These organisms have slower growth, longer life spans, and larger adult size. While organisms subject to K- selection are commonly assumed to have lower tolerance limits to physical perturbations, they conventionally are assessed as superior competitors.

Sanders (1968) formalized two community types influenced by environmental characteristics. A "physically controlled" community may be found in regions with unfavorable and/or widely fluctuating physical conditions. The evolutionary response induced by these conditions would be to withstand physical stresses and to recover rapidly from large perturbations. A "biologically accommodated" community may be associated with a physical environment that is constant over long periods of time. Subtle adjustments may be made to the local environment, and adaptations in organisms are in response to biological interactions.

The Stability-Time Hypothesis has been suggested to explain the species-diversity patterns of natural communities (Sanders Ibid.). Central to the theory is that species-diversity decreases with increasing physical severity. Organisms inhabiting physically controlled areas must adapt to physical conditions, precluding adjustments to biological stresses. When biological interactions occur in physical communities, stable outcomes are not expected (Sanders Ibid.,

1969; Slobodkin and Sanders (1969).

Slobodkin (1968) reasoned somewhat differently concerning the relative importance of environmental rigor and predictability in determining community structure. Mechanisms mitigating biological interactions would be strongly selected for if physical perturbations were both predictable and frequent relative to the organism's life span. If fluctuations could not be anticipated, broad tolerance limits would be selected as the evolutionary response (Slobodkin and Sanders op. cit.). Predictability was assessed as the primary agent limiting the types or organisms that can persist in an environment.

Organisms inhabiting low-diversity "physically controlled" regions are assumed to be inferior competitors, and therefore are excluded from more benign habitats by competition with biota of high-diversity "biologically accommodated" communities. Species of low-diversity locales have been described as "the cosmopolitan forms and tend to be the weed or fugitive species" (Slobodkin and Sanders 1969: p. 84).

Invasions by highly competitive species from biologically accommodated communities may be a major source of mortality to biota in physically controlled environments during periods of highly stable physical conditions (Obrebski pers. comm.). However, during episodes of physical stress in biological communities, mortality will result from the stresses, not from the invasion of biota of physically controlled communities. Baker (1910: p. 67) anticipated this by

stating: "On the whole it seems as though the greatest competition has been called into play in the lowest zones, the dry and uncongenial regions of the upper shore being left to the most tolerant forms, which, if left to themselves, are able to grow anywhere on the shore."[1]

Relative to the remaining intertidal regions, the littoral fringe represents the most physical and unpredictable environment in the Sanders sense. Evidence supporting this hypothesis is the documented catastrophic mortalities in high intertidal limpets from physical extremes (Lewis 1954; Frank 1965; Sutherland 1970). Life history patterns of littoral fringe organisms should reflect adaptations to the physical environment.

The population dynamics described for Littorina planaxis are not those predicted for an r- strategist. High fecundity is a characteristic, although reproduction for many seasons is not. A small egg is often associated with r- selection since dispersion of gametes is important in recolonizing. However, Grahame (1973b) maintained that species with long life spans will have a lower portion of assimilated energy channeled into reproductive products (i.e.: eggs, capsules) than short-lived species. Long-lived organisms use significantly more energy for maintenance, a characteristic not

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[1] The original literature was not seen. This passage was taken from Connell 1972.

associated with r- strategists. Littorina planaxis has several traits that are characteristic of K- strategists. These include long life span, slow growth, and moderate size of the adult. Conversely, L. planaxis has broad tolerance limits to many physical stresses and inhabits areas subject to density-independent mortality.

It is apparent that the concepts of r- and K- reproductive strategies do not apply to the Littorina planaxis life history. These concepts may be of minimal value in describing the littoral fringe habitat. Clearly r- and K- selection are useful concepts in describing life history patterns of organisms recolonizing an environment following a major perturbation. A temporal succession may be precluded in physically stressed environments where a limited number of species types can persist. Following catastrophic mortality of littoral fringe organisms, resources are not available for recolonization by species with low tolerance abilities. Using r- and K- selection to make spatial comparisons of life histories between different habitats may not be useful. These strategies imply that interactions occur between the two species types. Thus, a K- strategist may initially be disadvantaged by slow growth following a perturbation, but will eventually exclude r- strategists if no further perturbations occur. If, however, species are affected by factors independent of each other, the concepts of r- and K- selection are of little comparative value.

Murphy (1968) proposed mathematical and genetic models to

investigate advantages of iteroparity. He concluded that long life, late sexual maturity, and repeated reproduction were life history attributes associated with environments inhospitable to juveniles. Environments with low pre-reproductive survivorship are those with widely varying density-independent mortality rates and those with intense competition between young and adults. Long life and repeated reproduction will be selected under conditions of stable adult mortality and uncertain juvenile survivorship. Supporting evidence presented by Murphy (Ibid.) indicate that fish species having the greatest variation in reproductive success were also the longest lived. Littorina planaxis life history attributes validate Murphy's conclusions.

Frank (1968) maintained that the reasons for the large number of longevous species in stable communities are not known. However, Frank did not consider that adult and juveniles of the same species may have different tolerance limits to environmental stresses. Under conditions of high juvenile mortality, regardless whether it stems from physical impact or biological interaction, the evolution of long life and iteroparity may be expected. Thus, highly stable communities may result from component species with life history patterns that reflect the low survivorship of juveniles.

Available data on the population dynamics of other high

intertidal gastropod species suggest that stability may be characteristic in this habitat. For example, Whitlatch (1972, 1974) found populations of the salt marsh snail, Batillaria zonalis, to remain numerically stable for considerable periods of time. Sutherland (1970) provided an interesting comparison of a species in two different environments. High populations of Acmaea scabra were less dense, but showed no seasonal fluctuation in abundance. Additionally, the snails were larger, longer-lived, and faster growing. Populations were composed primarily of older individuals. Recruitment into this zone was minimal, barely equalling adult mortality. Physical fluctuations were a major source of mortality, occasionally reaching catastrophic proportions. Lower populations had seasonal fluctuations in abundance, higher recruitment success, and higher mortality rates. Individual growth rates were lower and snails were much smaller in size.

The life history pattern of Littorina planaxis may be the result of low pre-reproductive survivorship. Populations were observed to remain stable throughout the twelve months of the study. The average size of snail did not vary, nor did abundance or population age structure. Most populations were characterized by either middle or large size class predominance. No recruitment was observed during the study, and several populations may have suffered recurrent failure for many years. Individuals were found

to grow slowly, adding slightly less than 1mm in shell length per year on the average. Snails mature in two to three years at a size of 4.5 to 5mm in length. The average age of a L. planaxis was 11 years, corresponding to a 12mm shell length.

SUMMARY

1. Five study populations of Littorina planaxis were monitored for a twelve month period at Bodega Bay, California. Study sites represented a gradient in wave exposure rather than geographical area.

2. Abundance did not vary seasonally in any population. Mean abundance did vary from population to population, and appeared to be directly correlated with wave exposure.

3. Mean size of snail did not vary seasonally, but did vary on a population level. Small size classes contributed little to the population mean size snail.

4. Size-frequency distributions illustrated the paucity of small snails in all populations. Two distributions were recognized: populations with middle size class predominance, and those with large size class predominance.

5. Recruitment of young was not observed in any population. Size-frequency distributions indicate that recruitment failure may be common.

6. A survey of all populations at Dillon Beach revealed only one with a significant number of young. The topography of the rock containing the juveniles was considerably different from other areas; the surface had many small pits that were occupied by juveniles.

7. Growth of individuals decreased with increased size. A conventional growth curve was fitted to the data, and indicated that L. planaxis is quite longevous: mean age was 11 years.

8. Snails grow to approximately 3mm in the first year, reaching 5mm in two to three years. Average annual growth increment was calculated to be slightly less than 1mm/year.

9. Two growth seasons can be recognized for Littorina planaxis correlated with breeding and non-breeding seasons. Growth was significantly reduced during breeding season.

10. Snails matured at 4.5 to 5mm in shell length, indicating L. planaxis is an iteroparous species.

11. Copulation was observed in all months of the year except October and November, although the frequency in winter months was quite low. Extensive pairing began in March and ended in early August.

12. During breeding season, snails in the field demonstrated a semilunar pattern of copulation. The frequency of pairing decreased with increasing wave action and when water was not available.

13. Females release eggs in the laboratory in many positions, not the position described for many other littorinids. Water was essential to induce spawning.

14. Females released eggs in the laboratory during five months: March through early August. Residual spawning was observed in several winter months.

15. A semilunar pattern of eggs released was noted for female snails during the breeding season. Laboratory experimentation indicated that L. planaxis does not have endogenous lunar rhythm, but spawn when water is available.

16. Laboratory experiments indicated that females release eggs 4 hours before predicted time of highest spring tide in the field, and finished by time of highest tide. If snails were placed in water at time of highest high tide, females would not spawn until the next highest high tide, 25 hours later.

17. The relationship between size of female and number of eggs produced in a lunar period was exponential. The average number of eggs released by a 13mm snail in one lunar period is 14,200 eggs.

18. The yearly fecundity was calculated by multiplying the number of eggs released per size class in one lunar period by the number of lunar periods in a breeding season. The yearly fecundity of a 13mm snail was 113,600 eggs.

19. Available data on the reproductive characteristics of the genus Littorina were analyzed to discover correlations among life history parameters. It was found that littorinids have 4 major reproductive strategies correlated with position in the intertidal zone.

20. High intertidal species tended to have planktotrophic or ovoviviparous development, egg capsules containing a single small ovum, and high fecundity.

21. The life history attributes of L. planaxis validated Murphy's (1968) predictions that long life, late sexual maturity, and iteroparity are associated with habitats inhospitable to juvenile survival.

22. The inapplicability of r- and K- selection concepts to the populations studied are discussed.

23. The present study supported Dayton's (1970) theory that community structure may be determined by environmental conditions of the adult habitat, not necessarily that of the larval stages. The virtual lack of recruitment into populations of Littorina planaxis reflects the severe impact of environmental conditions on juvenile survivorship.

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